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LARGE MAMMALIAN PREY — PREDATORS IN BANDIPUR[1]

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(With eight plates & fourteen text-figures)

Large mammalian prey species and predators were studied in a 32 Km² area around Bandipur village in the Bandipur Tiger Reserve, Karnataka, between August 1976 and July 1978. Chital (*Axis axis*) comprised 69% and sambar (*Cervus unicolor*) 13 to 14% of prey number. The fertility rate of chital does was 1.3 and that of sambar does was 1. The average biomass of the hoofed prey species was 3320 Kg/Km²; including elephant (*Elephas maximus*) the average ungulate biomass was 9831 Kg/Km².

Dholes (*Cuon alpinus*) accounted for 80%, leopards (*Panthera pardus*) 15% and tiger (*Panthera tigris*) 5% of the 379 kills collected. Ratio of predator to prey biomass was 1:124. Annually the predators removed nearly 20% of the standing crop of the hoofed prey. This high predation rate was possibly because of the sudden removal of 100+ cattle from the study area which were grazing till the beginning of the study.

Hunting habits of dholes are described. Antipredator behaviour of the prey species, their ecological adaptations to breeding, biomass, and various ecological parameters which separate the predators are discussed. Calculations on the effect of predation on chital and sambar and the impact of stealing kills are presented.

INTRODUCTION

In the last two decades some important field studies on the large carnivores have been conducted in the Indian subcontinent (Fig. 1 and Table 1). Species studied include leopard *Panthera pardus* (Eisenberg and Lockhart 1972, Muckenhirn and Eisenberg 1973, Seidensticker 1976a), sloth bear *Melursus ursinus* (Eisenberg and Lockhart 1972, Laurie and Seidensticker 1977), tiger *Panthera tigris* (Schaller 1967, Seidensticker 1976a, McDougal 1977, Panwar 1979, Sunquist 1981) and lion *Panthera leo persica* (Joslin 1973, Berwick 1976). The techniques adopted varied from natural history observations (Schaller 1967,

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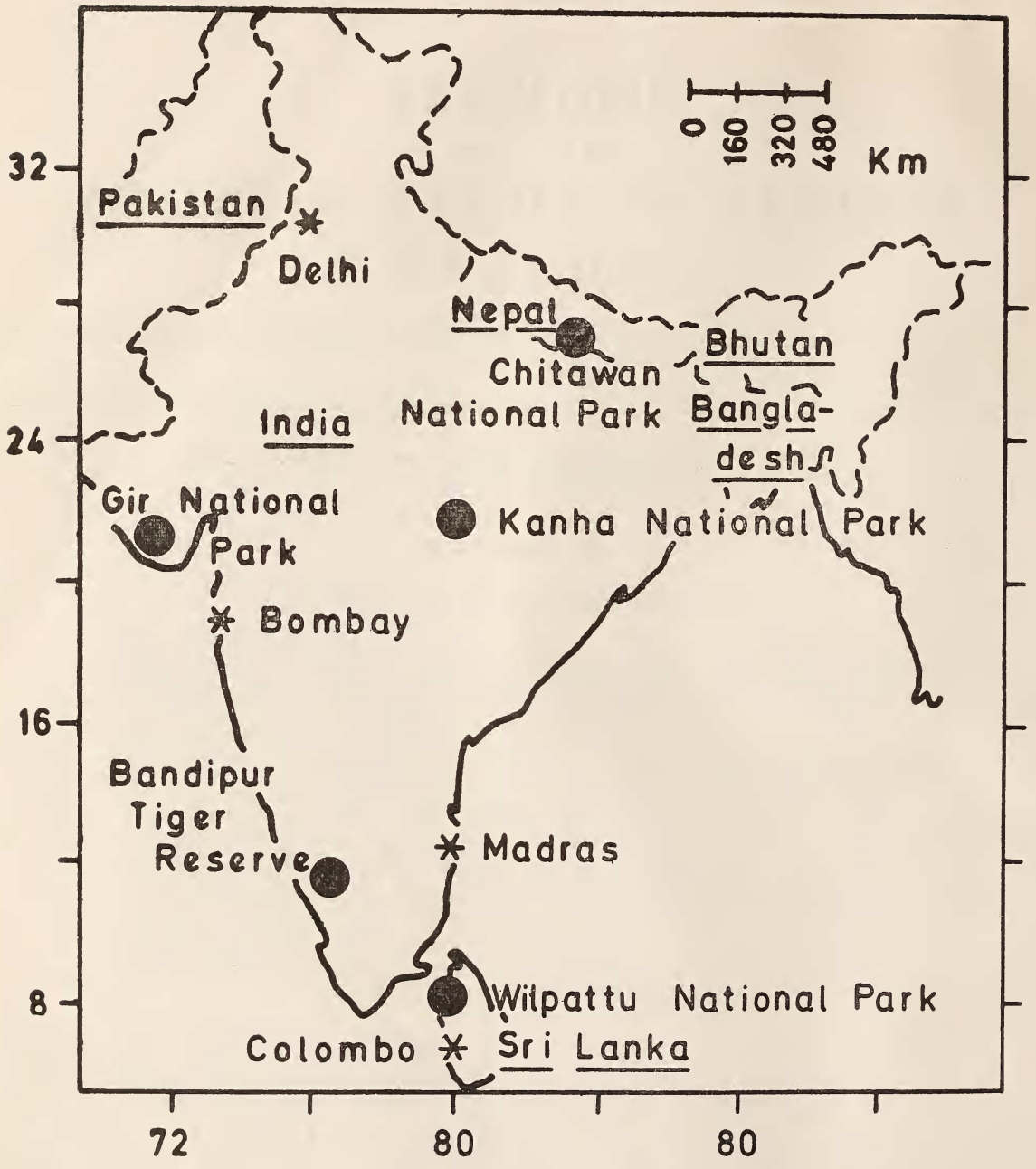


Fig. 1. LOCATIONS OF LONG-TERM STUDY SITES OF CARNIVORES IN THE INDIAN SUBCONTINENT.

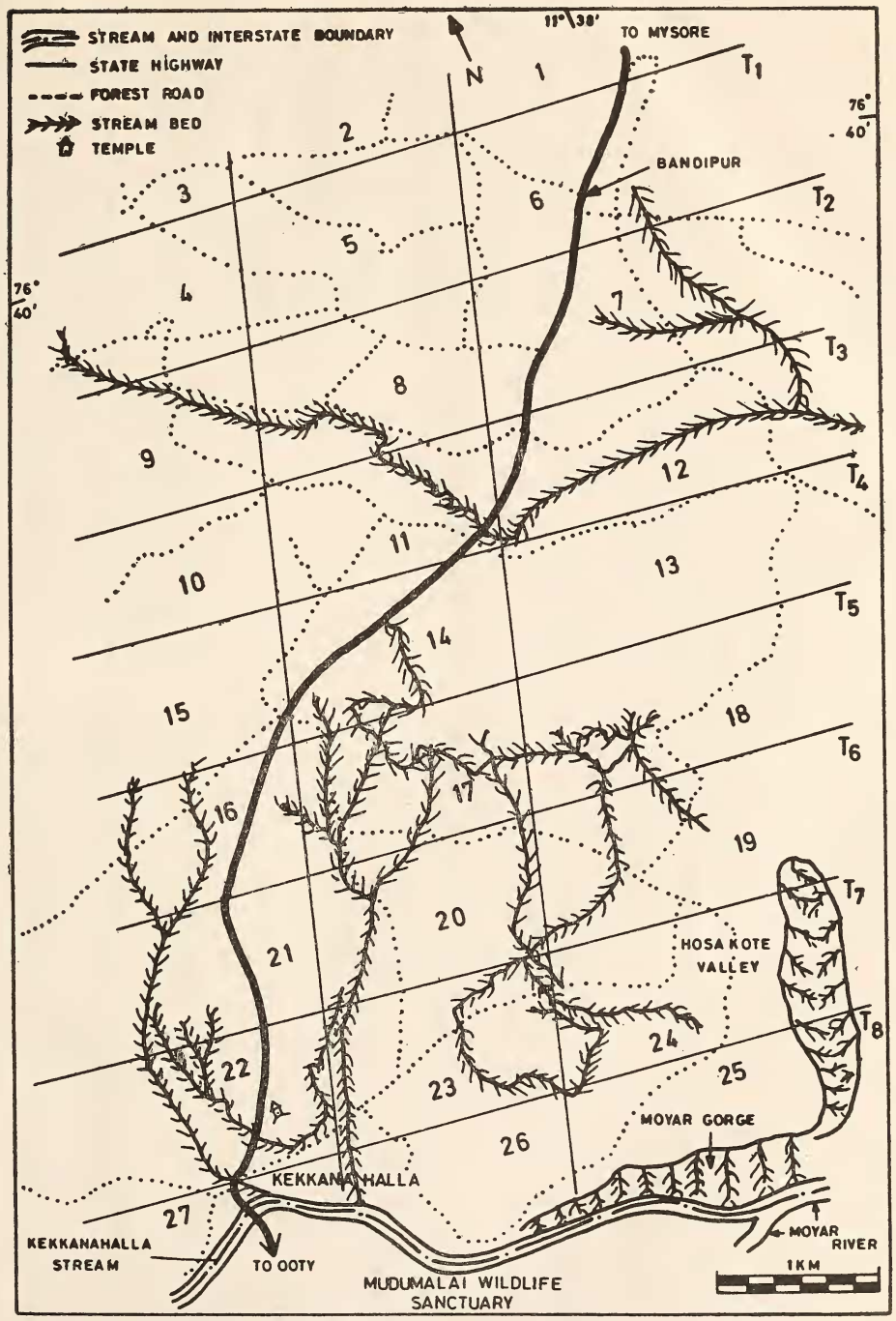


Fig. 2. Transect lines (T) and sectors of the study area.

TABLE 1

MAJOR LONG TERM STUDIES OF THE CARNIVORES IN THE INDIAN SUB-CONTINENT

Author	Study Site	Major floral characteristics of the study site	Major aspects of the study
Schaller 1967	Kanha National Park, Madhya Pradesh	Grass meadow — Sal forest	Tiger and its prey species
Panwar 1979	"	"	Population dynamics and land tenures of tigers
Joslin 1973	Gir National Park, Gujarat	Dry deciduous scrub jungle	Ecology of the Asiatic lion
Muckenhirn and Eisenberg 1973	Wilpattu National Park, Sri Lanka	Littoral monsoon scrub and monsoon forest	Home ranges and predation by Ceylon leopard
Seidensticker 1976	Royal Chitawan National Park, Nepal	Sal and riverine forest	Ecological isolation between tiger and leopard
Laurie and Seidensticker 1977	"	"	Behavioural ecology of the sloth bear
McDougal 1977	"	"	Ecology and behaviour of the tiger
Sunquist 1981	"	"	Social organization of the tiger
Present study	Bandipur Tiger Reserve, Karnataka	Dry deciduous forest, *Anogeissus latifolia* — *Tectona grandis* dominance	Ecology and behaviour of the dhole or Asiatic wild dog

Eisenberg and Lockhart 1972, Joslin 1973, Muckenhirn and Eisenberg 1973, Berwick 1976, Laurie and Seidensticker 1977, McDougal 1977, Panwar 1979) to radio telemetry (Seidensticker 1976a, Sunquist 1981).

I observed large ungulates and their predators in Bandipur from August 1976 to July 1978. The major purpose of this study was to assess the effect of dhole (*Cuon alpinus*) predation on chital (*Axis axis*) as Sharatchandra and Gadgil (1975) found dhole to be the major predator of chital and concluded that the chital population was declining. To compare the predatory habits of the dhole with those of the leopard and tiger kill data were collected for all three carnivores. Information was also collected on population density, movement patterns, reproduction, mortality, antipredator behaviour and biomass of the prey species.

Study Area

Bandipur, one of the 15 Tiger Reserves in India, offered an excellent opportunity to study the impact of dhole, leopard and tiger predation on chital and sambar (*Cervus unicolor*) and understand the ecological separation between a courser (dhole) and the stalking predators (leopard and tiger).

Because the study was carried out mainly on foot an area of 32 Km^2 was chosen around Bandipur (Fig. 2) and collection of kills, scats and prey censuses were restricted to the core area of the study pack, an area of 20 Km^2 (Fig. 3). Water in the study area was restricted to pools, some of which were perennial. Dense vegetation bordering pools and stream beds provided excellent cover for both ungulates and predators. The core area was divided into 219 quadrats for data analysis. In addition to the above mentioned animals the large mammal fauna in the Reserve included wild elephant (*Elephas maximus*), gaur (*Bos gaurus*), wild pig (*Sus scrofa*), muntjac (*Muntiacus muntjak*) and four horned antelope (*Tetracerus quadricornis*).

The vegetation was dry deciduous forest dominated by *Anogeissus latifolia* and *Tectona grandis*. Exotic weeds (*Lantana camara* and *Eupatorium glandulosum*) had established in many places. Bamboo (*Bambusa arundinacea* and *Dendrocalamus strictus*) regeneration was poor, after flowering in 1964 (Spillett 1966). Krishnan (1975a) gives a detailed account of the vegetation of Bandipur. The vegetation cover of the core area was classified into short grass scrub tree jungle (98 quadrats), scrub tree jungle (97 quadrats) and tall grass tree jungle (24 quadrats). Eleven of the 219 quadrats had permanent pools (Fig. 3).

Heavy premonsoon showers began in late April and May and the south west monsoon commenced in June and ended in August. The north east monsoon began in the later part of September and extended through November. Three seasons hot, wet and cool were distinguished (Neginhal 1974). The cool season started in November and lasted until mid February. During this period temperature seldom exceeded 25°C, relative humidity at noon was 70% and there was enough light to make field observations until 1800 h. Vegetation was green and dense after the retreat of the north east monsoon. Within a month, however, the grass turned yellow and began to seed. In January Forest department personnel burnt the road side grass and fire watchers patrolled the area during February, March and April.

The hot season commenced in late February and lasted until the middle of April. During March, the hottest month, temperature rose to 30°C even in shade and humidity was 42%. Sunset was around 1835 h. and there was sufficient light for field work until 1900 h.

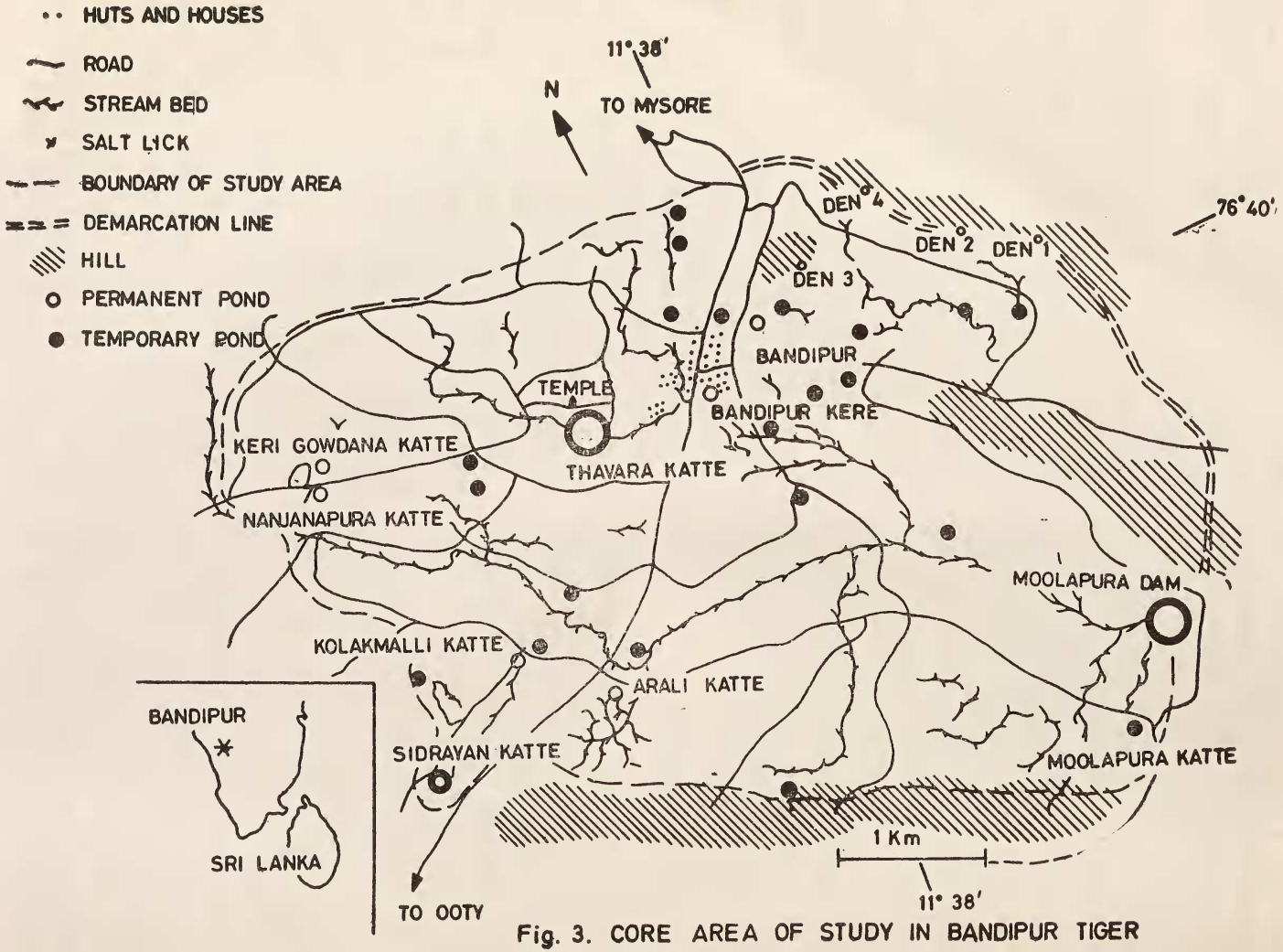


Fig. 3. CORE AREA OF STUDY IN BANDIPUR TIGER RESERVE

The wet season was the longest, extending from May to October. The sky was overcast throughout, temperature seldom exceeded 27°C and humidity rarely went below 60%. From the beginning of April premonsoon clouds drifted across the study area and showers activated the emergence of winged termites (*Odontotermes* spp.) and swarms of butterflies.

METHODS

GENERAL

The study was conducted between 1st August 1976 and 13th December 1977 and 4th February 1978 and 31st July 1978. Two local tribesmen served as field assistants throughout the study. Working on foot afforded an excellent

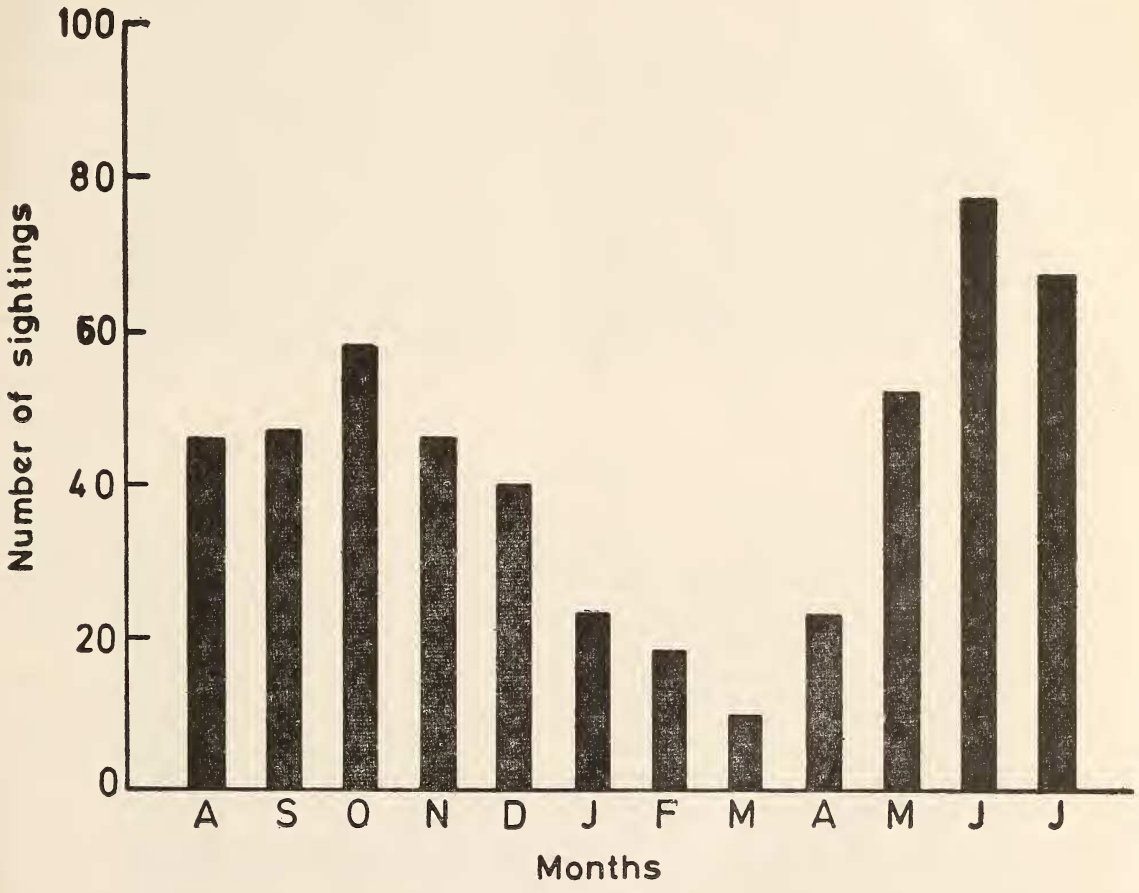


Fig. 4. Sightings of elephants, solitary as well as herd, from August 1976 to July 1977 (512 sightings).

opportunity to understand the terrain and its microhabitats but it imposed severe limitations on mobility. Elephants were common in the study area (Fig. 4) and their presence eliminated the possibility of working at night.

Twenty nine sites safe from elephants were used as observation points. The daily schedule began at 0630 h. when 3 observers went off in different directions looking for dholes. Observers stayed in one of the observation points or walked listening for the alarm calls of chital, sambar, common langur (*Presbytis entellus*), Peafowl (*Pavo cristatus*) and Grey jungle fowl (*Gallus sonneratii*). Jungle Crows (*Corvus macrorhynchos*) were of great help in locating kills. Fifty five per cent (n = 219) of fresh dhole kills, 72% (n = 58) of leopard kills and all (n = 19) tiger kills were located by observing crows. Tracking resumed again between 1500 h. and 1800 h. During the midday heat we searched the scrub for kills or remained in hides near water holes.

Whenever a prey species gave an alarm call we attempted to discover the cause when possible. For instance during the first year of study alarm calls of chital were heard 157 times, sambar 109 times and langur 56 times. Observations and indirect evidence helped to ascertain the reason only 12 times (8%) for chital alarms, 21 times (19%) for sambar alarms and 15 times (27%) for langur alarms. When alarm calls were recorded on the quadrats we acquired additional information on prey concentration and dispersion and preferred habitats of predators.

Whenever dholes were sighted we followed them at a distance of approximately 100 m. If a kill was made, the pack was approached as close as possible without detection, and while the pack was feeding it was possible to observe them for longer periods of time. The pack size, location, weather and time of day were recorded at each sighting. Tiger and leopard numbers were assessed on the basis of sightings, tracks and location of different fresh kills.

Kills and their age estimation

In cases where direct observation was not possible the prey's wounds, tracks and trampled vegetation helped to determine the identity of the predator. Tiger kills were distinguished from leopard kills mainly by the tracks and hair seen around the kill.

Whenever possible kill remains were weighed to estimate amount of meat eaten. Lower jaws were collected and teeth were inspected for dental deformities. Size and condition (velvet or hard) of antlers were also recorded.

Eruption and wear of premolar and molar teeth was used to determine the relative age of prey. Chital were classified into 9 age categories (Schaller 1967) and sambar were classified as young fawns, large fawns, yearlings and adults. Fawns with erupting premolars were classified as young fawns. Fawns with fully erupted milk premolars were considered large fawns. Sambar fawns completely eaten by dholes were also included in the young fawn group.

Six chital carcasses were checked for ecto- and endoparasites. Lungs of 9 partly eaten chital and of 2 sambar fawns were checked for parasitic cysts.

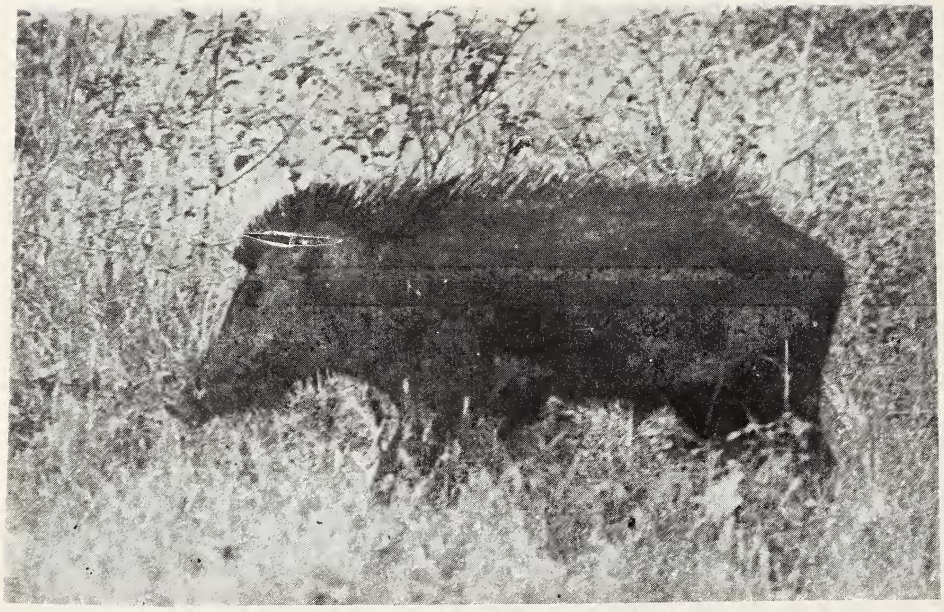
Scat study

Dholes use scats for marking their home ranges and one or two scats were, therefore, collected from latrine sites. It was assumed that fresh droppings represented the previous meal and I was thus able to investigate the sequence of kills.

A herd of chital in a pool in Bandipur.

Sambar leaving a pool.
(Photos: *Author*)

A gaur herd in Bandipur tree jungle.



Wild pig - dominant mammalian scavenger in Bandipur.
(Photos: *Author*)

Leopard and tiger defecate either on the central grassy strip of forest roads or on grass immediately bordering them. These areas were searched for scats.

The scats were later soaked in water and dissected thoroughly to separate hair, bones and other components. Hair samples donated by Bombay Natural History Society and those collected from kills were used as reference. Whenever identification was not possible with the naked eye a binocular microscope and the key by Koppikar and Sabnis (1976) were used.

Adult and fawn remains in scats were visually differentiated by the nature of the hair, presence of hooves teeth and digested calcium. Presence of soil and grass was taken into account if 50% or more of the droppings consisted of these items (Schaller 1967). When the remains of more than one species was found in a scat, all hair types were identified and all species that had contributed to the scat content were considered eaten by dholes. A total of 509 dhole, 70 leopard and 36 tiger scats were collected. Sixty seven scats of jungle cat

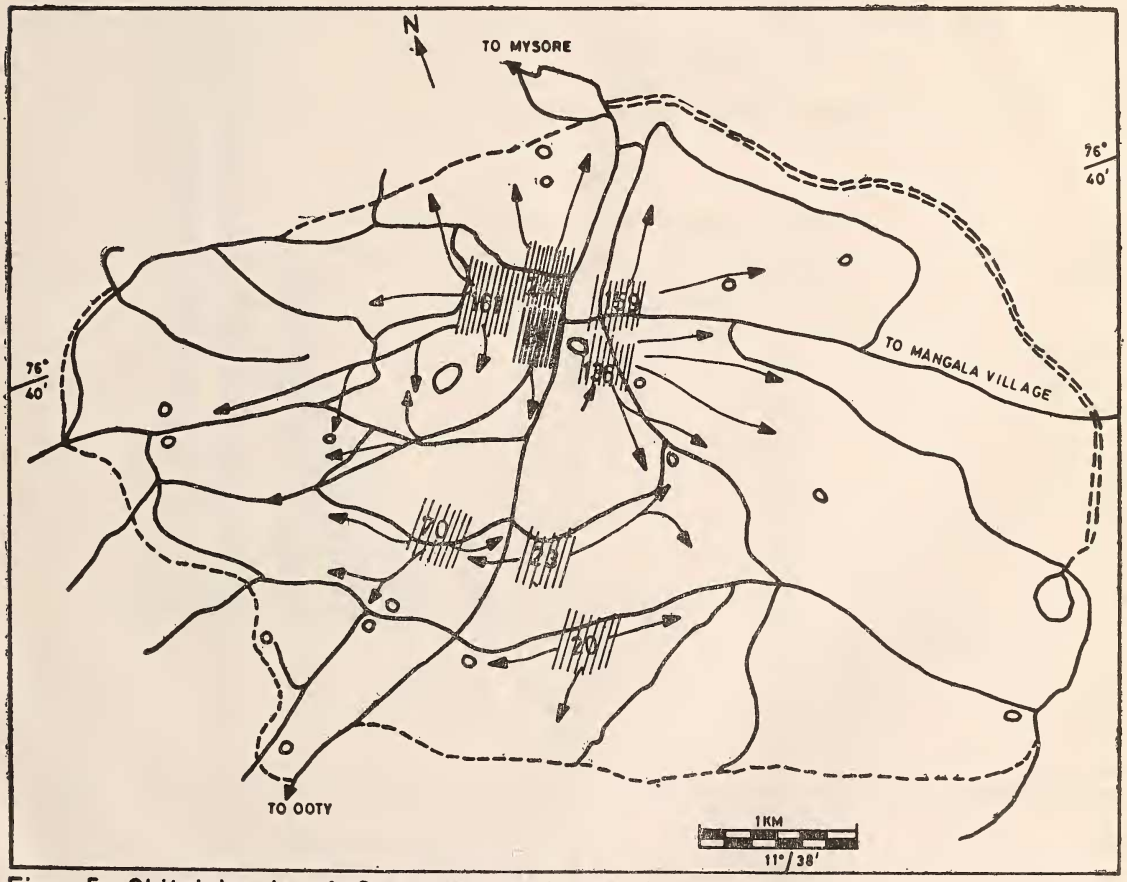


Fig. 5. Chital herds of Core area and directions of their foraging trips from their rest sites (July 1977).

(*Felis chaus*) and 86 of sloth bear were also analysed.

Prey density estimates

Population estimates of prey species were based on direct counts. In Bandipur from May to October chital formed large herds in certain parts of the core area (Fig. 5). In these months nearly 500 chital from Sommayanakatte, Mysore lodge pool and Huvinkatte came to Bandipur campus to spend the night. They were counted from trees near trails either when they came to the campus or left.

Chital in other areas were counted either from vehicles or from a distance with binoculars. Counting was difficult during the dry season when chital were dispersed. Chital were classified as adult ♂♂ in hard and velvet antlers, yearling ♂♂ with spike antlers, does and fawns (Table 2). Males in shed antler were included in the velvet group.

Accurate estimation of sambar numbers is difficult as they prefer dense cover and are solitary or found in small groups (Fig. 6). In undisturbed parts of the study area sambar were active during the day, but in disturbed areas they retired to cover at day break and emerged late in the evening. Sambar were counted and observed as they came out of cover in the evening to feed and when they returned to rest sites. From May to September sambar visited waterholes during the day time more frequently than in other months ($X^2 = 34.57$, d.f., 1,

Table 2

Age and sex ratios of chital counted in the core area

Month	Total number counted and classified	Spike/Stag	Total male/ Total female	Fawn/ Female
August, 1976	701	0.15:1	0.57:1	0.28:1
September	629	0.25:1	0.62:1	0.37:1
October	525	0.31:1	0.4 :1	0.38:1
November	708	0.42:1	0.63:1	0.42:1
December	510	0.24:1	0.47:1	0.39:1
January, 1977	508	0.25:1	0.68:1	0.44:1
February	504	0.20:1	0.59:1	0.42:1
March	521	0.24:1	0.74:1	0.60:1
April	643	0.47:1	0.52:1	0.53:1
May	740	0.32:1	0.81:1	0.70:1
June	910	0.28:1	0.77:1	0.66:1
July	857	0.32:1	0.93:1	0.67:1
August	935	0.51:1	0.69:1	0.58:1
September	801	0.39:1	0.85:1	0.53:1
October	619	0.51:1	0.85:1	0.44:1
November	756	0.49:1	0.84:1	0.42:1
February, 1978	332	0.28:1	0.49:1	0.29:1
March	361	0.09:1	0.51:1	0.33:1
April	872	0.53:1	0.62:1	0.49:1
May	1096	0.34:1	0.72:1	0.61:1
June	1114	0.33:1	0.81:1	0.60:1
July	1172	0.33:1	0.86:1	0.63:1

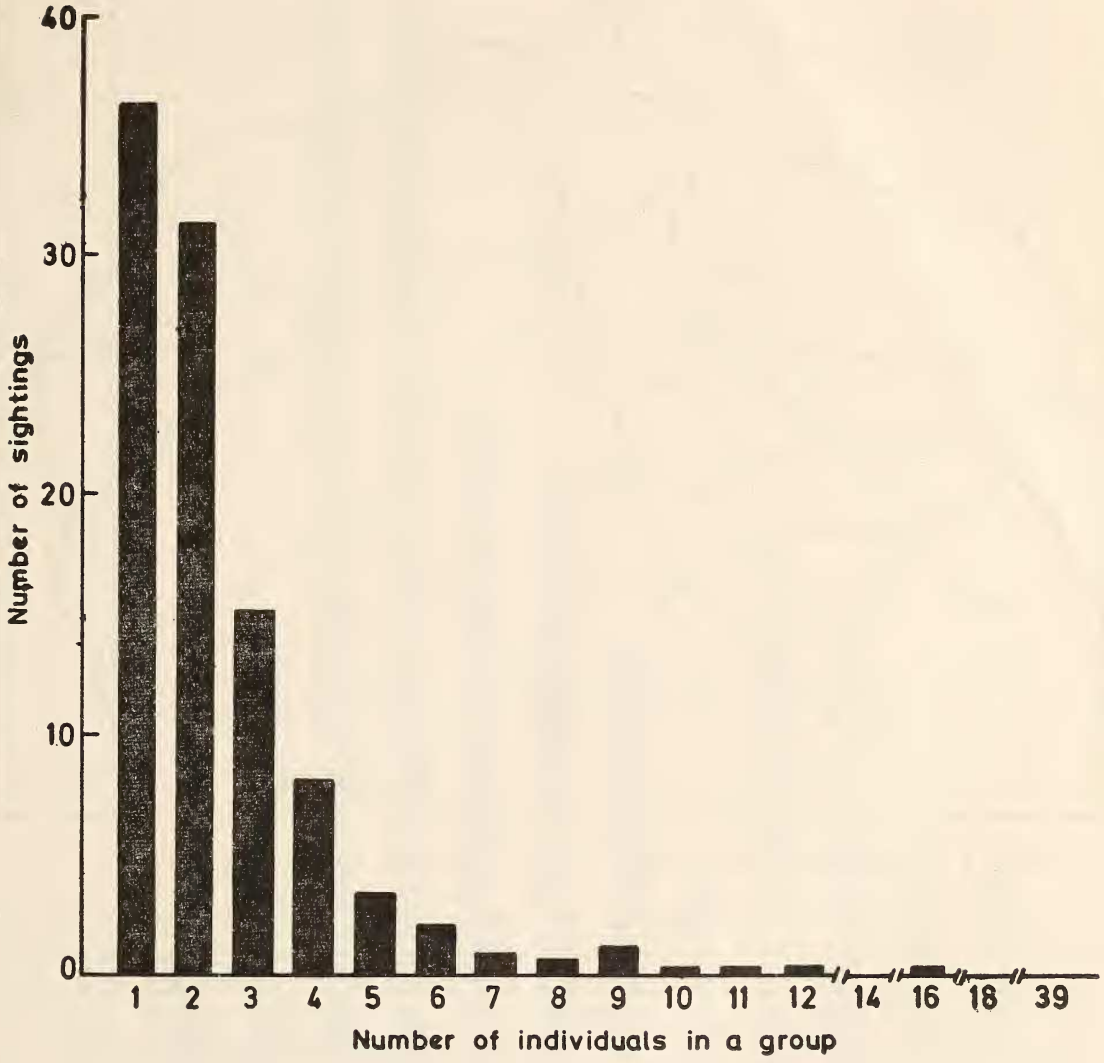


Fig. 6. Frequency of sightings of sambar groups of various sizes (Total 1995 sightings).

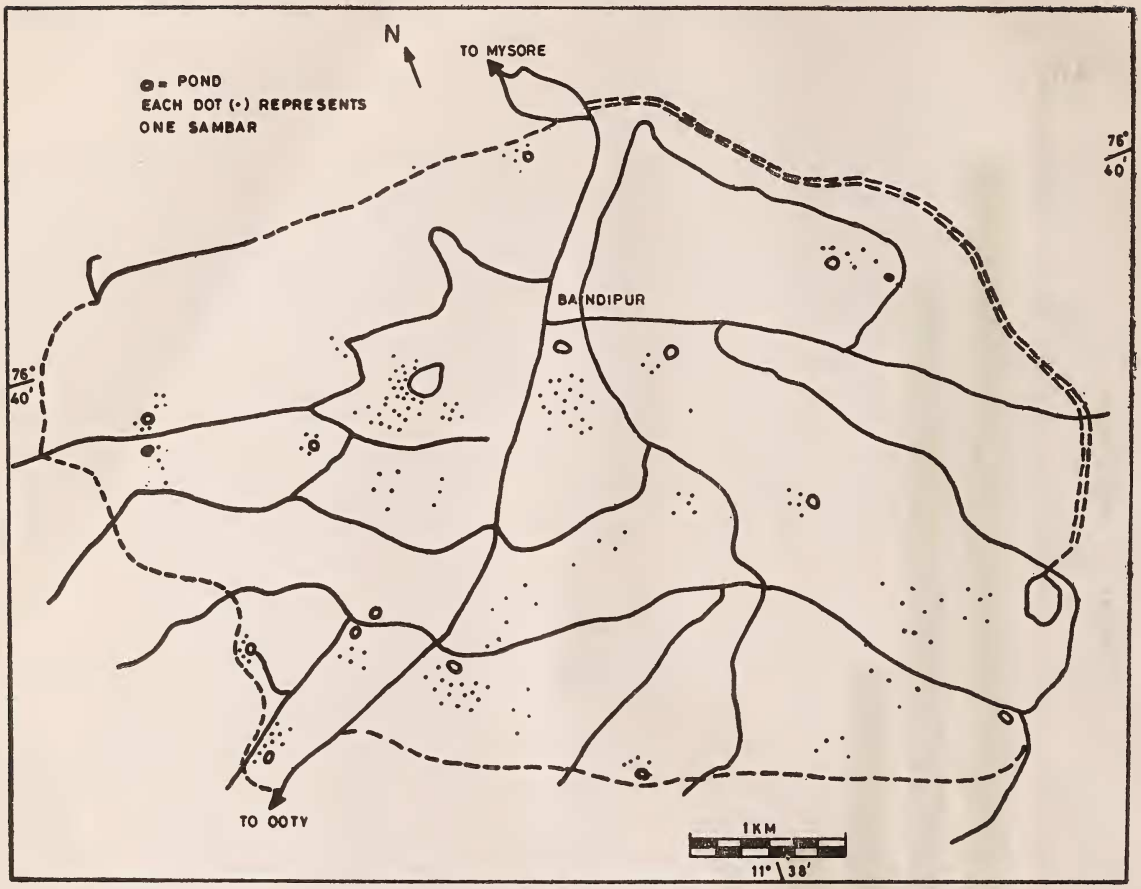


Fig. 7. Concentrations of sambar in the Core area during July 1977.

$P < 0.001$, Table 3). Preferred localities of sambar are marked in figure 7. Sambar were classified into adult ♂♂ in hard and velvet antlers, yearling ♂♂ with spike antlers, does and fawns (Table 4).

The abundance of other prey species including elephants, gaur, wild pig, muntjac, common langur, porcupine (*Hystrix indica*) and Black-naped hare (*Lepus nigricollis*) was also estimated. Peafowls were counted at roost sites.

A line transect study was carried out in other parts of the study area to document the abundance and seasonal migration of prey species. Eight 4000 m long transects were laid out at intervals of 600 to 800 m (Fig. 2). Every month from September 1976 to August 1977 ungulate counts were made from these transects. The study area was then divided into 27 sectors and sightings were recorded on the map. In addition a monthly watch was kept on waterholes between October 1976 and August 1977. Animals were counted as they came to drink between 0900 and 1600 h. two days each month (Table 3). Temperature, humidity and

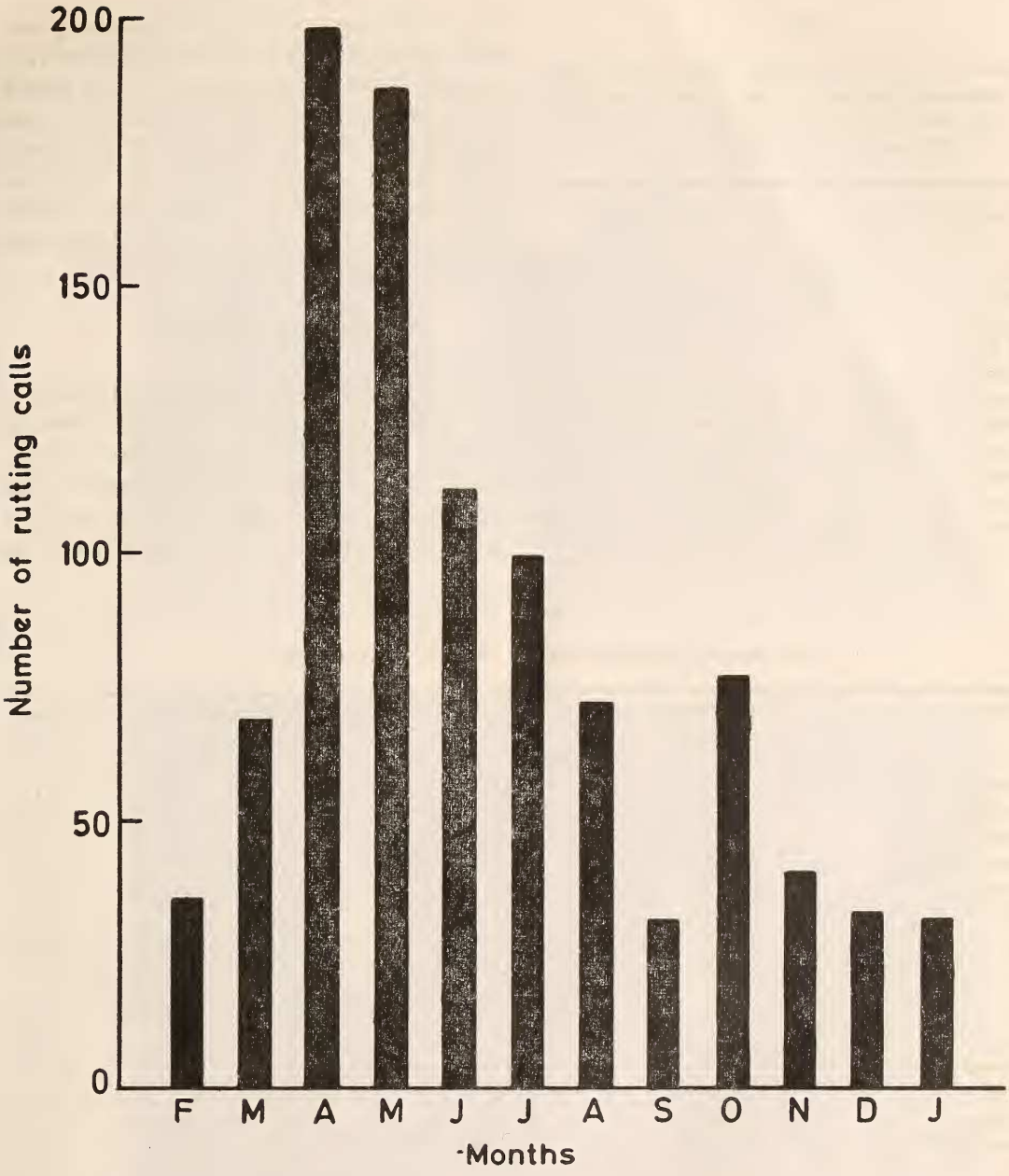


Fig. 8. The total number of rutting calls of chital stags heard daily between 0630 and 0930 h and between 1600 and 1830 h over the period February 1977 to January 1978.

Table 3

Number of large mammalian herbivores visited the waterholes during the dry season (5 months) and the wet and cool season (6 months) — (October 1976 to August 1977)

Wet and Cool Season		Dry Season	
Chital	20		284
Sambar	50		5
Muntjac	—		10
Wild pig	1		1
Langur	—		1
Maximum humidity	77	Maximum humidity	77
Minimum humidity	36.5	Minimum humidity	20
Maximum temperature	28.5°C	Maximum temperature	32°C
Minimum temperature	21°C	Minimum temperature	19°C

time of visit were recorded. Observation points were chosen in such a way that the observer's presence could not be detected. Chital rutting calls were counted between February 1977 and January 1978 (Fig. 8). Jungle cat (*Felis chaus*), jackal (*Canis aureus*), stripe necked mongoose (*Herpestes vitticollis*), Indian rock python (*Python molurus*) and Crested Hawk-Eagle (*Spizaetus cirrhatus*) were also observed.

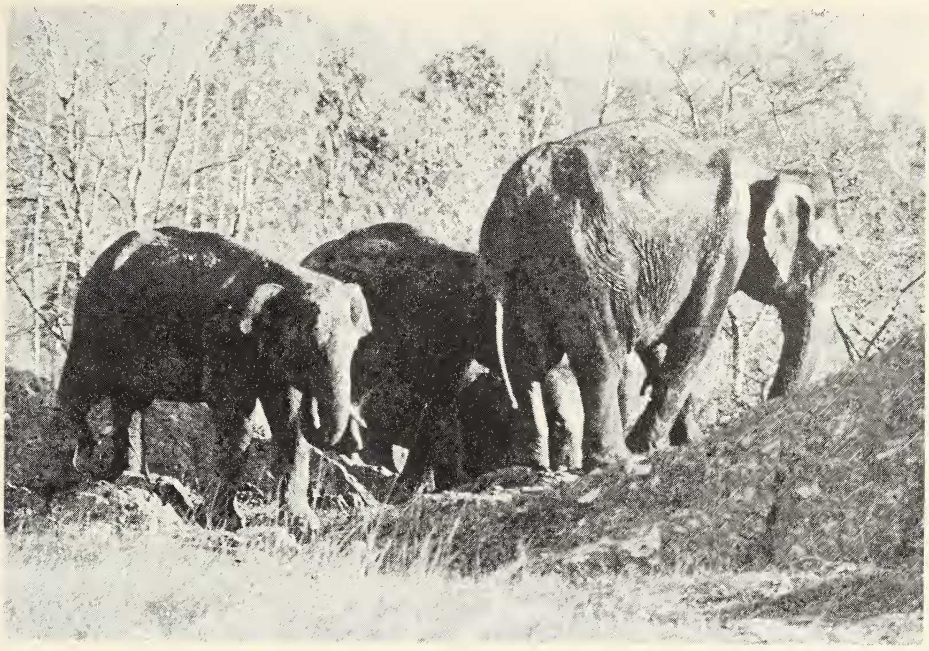
Biomass estimation

While estimating the weight and biomass of the species the procedure largely following Schaller (1967, 1972) was adopted. In elephants, gaur, sambar and chital there is large variation in size of different sexes and sex ratio. The biomass was calculated based on

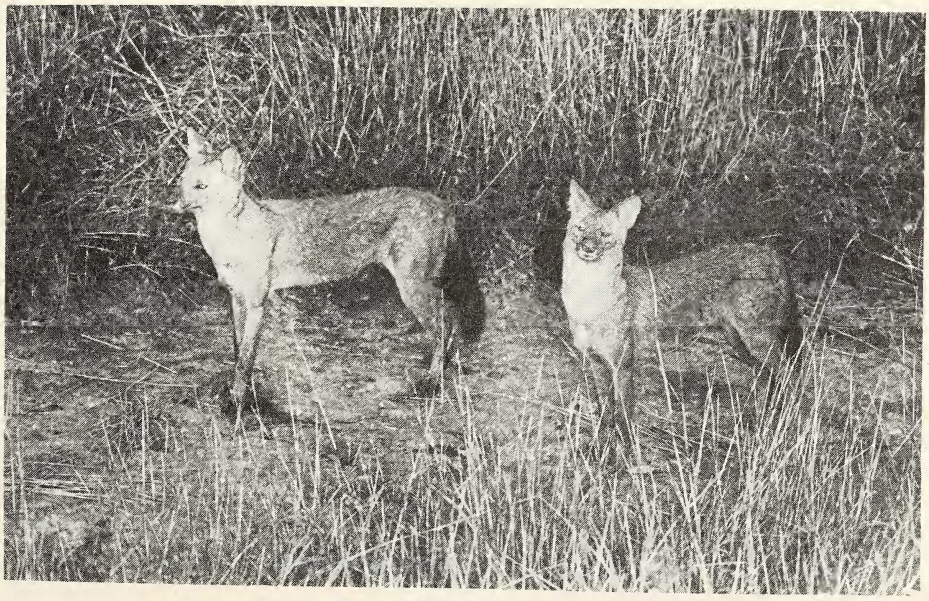
Table 4

Age and sex ratios of sambar seen in the core area

Month	Total number classified	Spike/Stag	Total male/ Total female	Fawn/ Female
October, 1976	140	0.43:1	0.49:1	0.11:1
November	211	0.25:1	0.37:1	0.20:1
December	174	0.19:1	0.44:1	0.31:1
January, 1977	182	0.18:1	0.43:1	0.27:1
February	142	0.26:1	0.50:1	0.37:1
March	144	0.32:1	0.37:1	0.25:1
April	162	0.56:1	0.29:1	0.40:1
May	315	0.47:1	0.43:1	0.36:1
June	315	0.56:1	0.41:1	0.33:1
July	379	0.68:1	0.50:1	0.28:1
August	346	0.68:1	0.48:1	0.29:1
September	253	0.93:1	0.33:1	0.21:1
October	229	0.70:1	0.50:1	0.32:1
November	164	1 :1	0.33:1	0.25:1
February, 1978	56	2 :1	0.16:1	0.35:1
March	99	1.2 :1	0.33:1	0.30:1
April	161	0.76:1	0.29:1	0.26:1
May	263	0.36:1	0.34:1	0.35:1
June	448	0.42:1	0.24:1	0.43:1
July	254	1.10:1	0.34:1	0.44:1



An elephant family group in Bandipur. The matriarch is drinking from a rock puddle.



Dholes have an excellent sense of smell.
Dhole on the right hand side tried to smell out the author's presence.
(Photos: *Author*)

Common langur was the prominent primate in Bandipur.

An alert pea hen. Peafowls are potential prey of large carnivores.
(Photos: *Author*)

the actual composition of the population. Weights of elephants were obtained from Mudumalai elephant camp (John Joseph pers. comm.) and for other animals data given in Prater (1971) were used. The biomass of langur, porcupine, hare and Peafowl was obtained by multiplying the three quarters of the weight of an adult ♀ by the number in the population. For pig and muntjac approximate minimum adult weight and number in the population was used. Since lone gaur bulls were mostly seen in the core area weight of an average sized bull was used.

Prey species

Chital

Density and population composition

Chital were the most common and conspicuous mammal of the study area. From May to October 857 to 900 chital congregated within a 7 to 8 Km^2 area around Bandipur and reached a density of 120/Km^2. These large herds fragmented at the onset of the dry season and formed bachelor herds, small groups of does and mixed parties. The dispersion of chital during the dry season may be influenced by a number of factors such as scarcity of green forage, availability of fruit and permanent water sources.

The movement pattern of chital in Bandipur (aggregation after rains) was different from that of Wilpattu where chital at the onset of rains dispersed from concentrations at selected villus (tank) toward villus which were dry during the drought (Eisenberg and Lockhart 1972). During the dry season it was estimated that nearly 800 chital remained in the core area, a dry season density of 40/Km^2. Density in Bandipur can be compared with the ecological density of 12.3/Km^2 in Bharatpur (Spillett 1967), 12/Km^2 in Wilpattu (Eisenberg and Lockhart 1972) and 17.3/Km^2 in Chitawan (Seidensticker 1976b). Extensive patches of short grass and dense thickets (fawning and escape cover) were the major reasons for the high density of chital in the core area.

Chital in Bandipur showed a sex ratio biased in favour of ♀ ♀ throughout the year. During the peak months of rut (1977 and 1978) the ♂ to ♀ ratio was 84:100. The highest fawn: doe ratio averaged for May, June and July 1977 was 68:100 and for the same period in 1978 the ratio was 61:100. In Bandipur 44% of the population was < 2 years old and for Kanha the figure was 53% (Schaller 1967).

Reproduction and peak in fawning

In Bandipur the peak rutting season was between April and July (Sharatchandra and Gadgil 1975 and Fig. 8). Extrapolating from the April to July rutting peak and assuming an 8 month gestation period (Schaller 1967) more fawns should have been seen from December to March. Young fawns, however, remained hidden during the early weeks and could only be reliably counted when they began to accompany the does. This occurred in May, June and July after the summer rains and sprouting of grass. Twin fawns were observed on 5 occasions.

Peak in fawning could be confirmed by distributing fawn kills, number of scats with fawn remains collected in Bandipur and fawn births recorded by Crandall (1964) over different months of the year (Fig. 9). In total 100 fawns killed by dholes, 11 by leopard and 1 by tiger were collected. Fawn remains were seen 143 times in dhole scats. Twenty five scats of leopard and 8 of tiger had fawn remains. When distributed over the year it was clear:

a) fawn kills showed a peak from February to July;

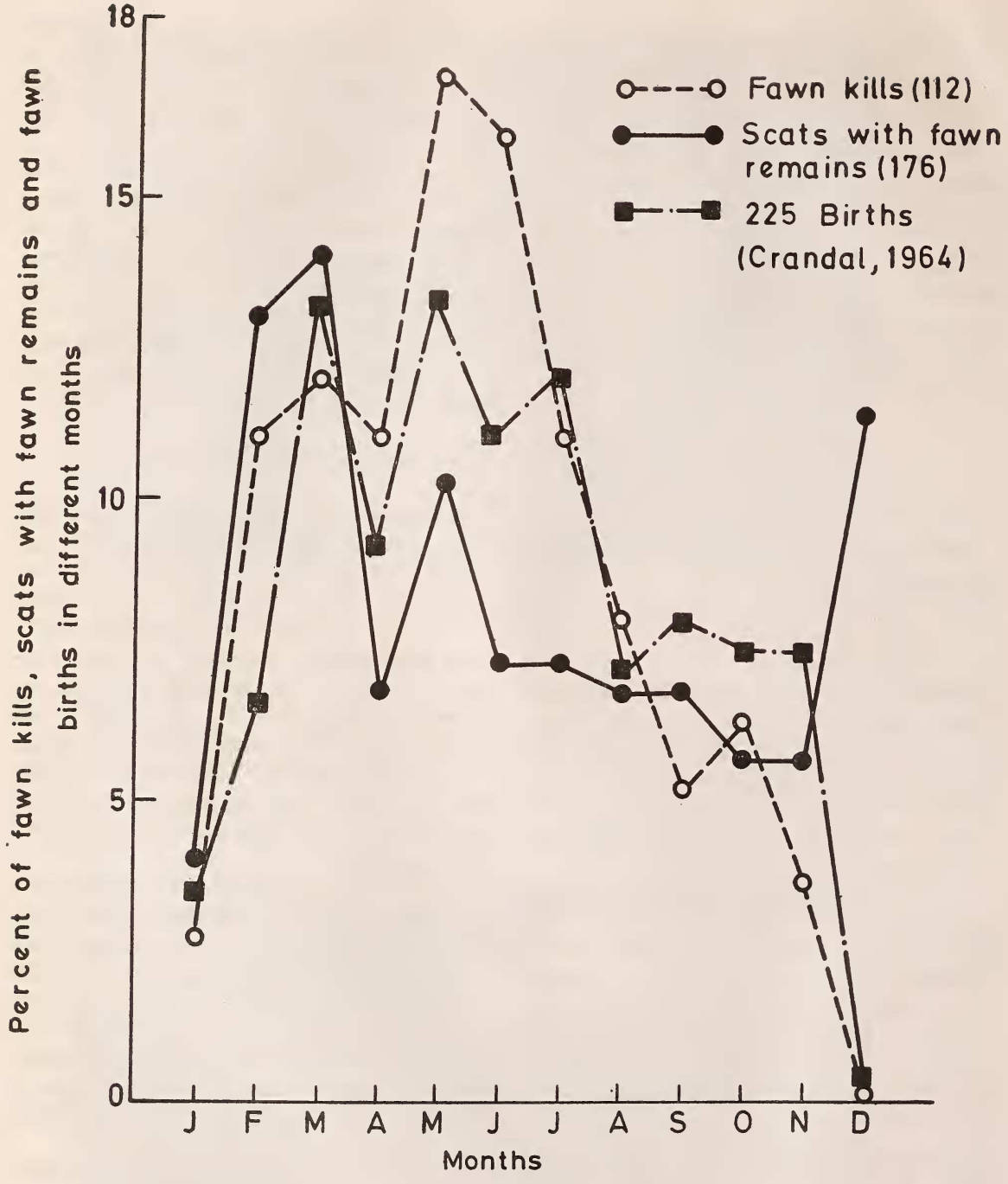


Fig. 9. Chital fawn kills, scats with fawn remains and birth of fawns in different months of the year.

b) scats with fawn remains were common in December, February and March;
c) birth of fawns showed a peak from March to July.

Young fawns are said to be scentless. (Brander 1927, Graf and Nicholas 1966). Scat analysis, however, showed that in December, February and March many fawns were killed than in other months ($X^2 = 25.885$, d.f., 1, $P < .100$). Pooled together the data indicated a fawning peak from December to March. Fawn sex ratio (Graf and Nicholas 1966, Schaller 1967, Acharjyo and Padhi 1972) indicates an even sex ratio at birth. Adult sex ratio however, favoured ♀ ♀ and this could be attributed to a higher mortality of ♂ fawns.

Mortality

Possible causes of mortality include accident, disease and predation. Two does and one stag were killed by vehicles. Deep wounds were frequently seen on rutting stags and one stag killed by dholes had a deep stab wound in the lower jaw. In May 1977 one stag was killed by another stag.

All chital examined had ticks (*Haemophysalis* spp) and flies (*Lipoptena* spp). Of the 13 checked for cysts, one young stag with 40 cm long hard antlers, had an infestation of 30 *Cysticercus* cysts in the lungs and a prime adult doe had 3 cysts and *Setaria* spp worms in its peritoneal cavity. Deformities which can affect feeding efficiency and lead to debility are listed in Table 5.

The major cause of mortality was predation. Chital accounted for 74% of the 379 kills by predators. An analysis of 509 dhole, 70 leopard and 36 tiger scats showed chital hair in 52%, 51% and 39% respectively.

Local people frequently stole kills of predators. This probably had a deleterious effect on chital population as predators were forced to make more kills. During August and September 1976 there were 18 dhole and 3 leopard kills of chital. All 3 leopard kills and 10 of the 18 dhole kills were stolen.

Antipredator behaviour

Chital have an excellent sense of smell and hearing but they often failed to detect me at distances of 5 to 7 m when I sat and froze close to a tree. They were alerted by the alarm calls of other animals, and sensed the presence of dholes which were not noticed by me (see Appendix I, hunt 17). When attacked by dholes (e.g., hunt 9) even chital with long hard antlers fought ineffectively. Chital employed a variety of antipredator strategies including:

(a) Bunching: Chital were seen to bunch in the presence of dholes ($n = 16$) and in the presence of leopard ($n = 2$) and tiger ($n = 1$). Bunching was seen 17 times in wet and cool months.

Dholes were not observed to attack chital in a herd. The fear of being trampled and the inability to concentrate on a particular individual may deter dholes. Stags on seeing dholes moved either to the front or to the middle of the bunched fleeing herd. When 7 dholes went past a herd of nearly 100 chital the stags ran to the middle and 4 to 6 chital does with raised tails and stamping feet came forward to investigate. Once a leopard walked by and nearly 25 chital bunched and with raised tail sounding alarm and stamping their forefeet trailed at a distance of 40 to 50 m behind the cat, similar to an incident reported by Eisenberg (in Smythe 1970). The behaviour of the chital was like the curiosity behaviour reaction of hoofed mammals towards African predators (Kruuk 1972).

(b) Distraction display: Does with young fawns ran off and left the fawn on two occasions. A doe with a young fawn as soon as it

TABLE 5

DEFORMITIES SEEN IN CHITAL KILLED BY PREDATORS

Sl. No.	Date or month	Particulars of Prey, Sex, age class and antler length in cm.	Deformity	Predator
1.	August, 1976	♀, VIII	Exerstosis on the left maxilla on the medial aspect at the first molar level. Both the first molars not well developed.	Dhole
2.	March, 1977	♀, VIII	Differential wear. No wear on the first premolar and heavy wear on the last molar.	Dhole
3.	12 June, 1977	♀, VIII	Differential wear. First premolar was not worn down. Possibly the upper apposing molar was absent.	Leopard
4.	1 August, 1977	Stag, V, 82 cm hard antlers	Excess callus formation at the junction between the last maxilla and the maxillary symphysis probably due to a piercing wound.	Dhole
5.	20 August, 1977	♀, VIII	Differential wear on molars. First premolar and last crown of the 3rd molar were not worn down.	Leopard
6.	January, 1978	Stag, V, Velvet antlers eaten	Congenital maldevelopment (hypoplacia) of the first molar on the right maxilla	Dhole
7.	28 February, 1978	♀, VIII	Differential wear conspicuous on the second molar on the left maxilla.	Dhole
8.	14 April, 1978	♀, VIII	Exerstosis on the right maxilla. Maldevelopment of teeth except the last molars.	Dhole
9.	21 June, 1978	Stag, V, 18 cm hard	Left antler of the stag had broken and had healed when it was in velvet at a height of 50 cm.	Dhole
10.	3 July, 1978	Stag, IV, 45 cm hard	First crown of the last molar and the last crown of the second molar were broken. Left antler was broken at a height of 12 cm from the base.	Dhole
11.	11 July, 1978	Stag, V, 72 cm hard	Extra third premolars	Dhole

saw me, lay flat on the ground and kept the head level with the grass. When I approached her closer she rose, spronked, heavily thumped her forefeet and the fawn ran away.

(c) Remaining motionless in cover: Adult chital sometimes hid in dense cover when alarmed by dholes (n = 3). One doe, took refuge in a bamboo clump when chased and attacked by a village dog in Sigur an adjoining forest tract. Chital fawns were also found hiding in dense cover (n = 7) (Appendix I, hunt 18). When chital were surprised in the scrub they gave a startled call and dispersed abruptly in different directions. This may confuse a predator.

(d) Flight: Chital flight distance varied in different parts of the study area. Near Bandipur they could be approached to a distance of 30 m but in the more remote parts of the study area, where poaching occurred, flight distances in excess of 80 m were common. When directly approached by hunting dholes the flight distance was usually 60 m or more. When pursued by dholes chital fawns called in distress.

(e) Seeking refuge in water: On 4 occasions during the study chital stood at bay in water to escape dholes but all were killed. Chital twice ran across the river in Sigur when pursued by dholes, probably in an attempt to lose them. On another occasion a chital doe stood at bay in Sigur river to evade a village dog. Only our intervention saved the doe.

Sambar

Distribution

Sambar were the most widely distributed large prey species in the study area. Their distribution and abundance appear to be influenced by dense cover, water and by their ability to subsist on a wider variety of plants. During the wet and cool season cover was afforded by *Lantana* and bamboo while grass *Imperata arundinacea* under shady trees (e.g., *Shorea talura*) provided cover during the dry months. Rest sites near water were preferred. In contrast with chital sambar were found in hilly terrain (e.g., sectors 3 and 19) and tall grass (e.g., sectors 10 and 15).

Group size, density and biomass

Sambar in the study area formed large groups only at water holes and feeding sites. Otherwise single animals and groups of 2 formed 36% and 31% respectively of the 1995 sightings. An unusually large aggregation formed in response to a dhole pack; a total of 39 sambar (6 stags in hard, 4 in velvet, 3 spike bucks, 19 does and 17 fawns) was observed standing in a pond where they sought refuge. The population estimate for the core area in July 1977 was 160 to 180 or a density of 8 to 9/Km^2. This concentration was not seen during dry months when nearly 140 sambar stayed in the core area which gave a dry season density of 7/Km^2.

The high wet season density of sambar formed 13 to 14% of the total number of prey animals (excluding porcupine, hare and peafowl) and 36 to 38% of the prey biomass excluding elephant. The wet season density gave a total biomass of 24, 875 to 27, 984 Kg. or 1244 to 1399 kg/Km^2 (Table 6). The related figure from Wilpattu is 158 kg/Km^2 (Eisenberg and Lockhart 1972) and Chitawan 443 Kg/Km^2 (Seidensticker 1976b). The high density in the core area was mostly due to dense patches of escape cover (*Lantana* and bamboo) around water holes, which are distributed evenly in the core area.

Sex ratio

Sex ratio of sambar at birth appears to be even; of the 35 births recorded by Acharjyo

TABLE 6

POPULATION DENSITY AND BIOMASS OF MAJOR PREY SPECIES (EXCLUDING PORCUPINE, HARE AND PEAFOWL) AND ELEPHANTS IN THE CORE AREA — JULY 1977

Species	Estimate of numbers	Density per Km²	Average weight used in computation (in Kg.)	Total Biomass	Biomass per Km²
Chital	857— 900 ♂ 307, ♀ 330, yg 220	43—45	♂ 50, ♀ 40, yg 20	32950— 34603	1648— 1730
Sambar	160— 180 ♂ 45, ♀ 90, yg 25	8—9	♂ 225, ♀ 150, yg 50	24875— 27984	1244— 1399
Gaur	10± 10±	0.5—0.5	800	8000— 8000	400— 400
Wild Pig	50± 50±	2.5—2.5	30	1500— 1500	75— 75
Muntjac	20± 20±	1—1	15	300— 300	15— 15
Langur	150± 150±	7.5—7.5	8	68825— 73587	60— 60
Total	1247 1310	62—65.5		219200—219200	3441— 3679
Elephant	100± 15 Tuskers, 41 Cows, 35 Juveniles and 8 Calves	5	Tusker = 4000 Cow = 3000 Juvenile = 1000 Calf = 150		10960—10960
Total				288025—292787	14401—14639

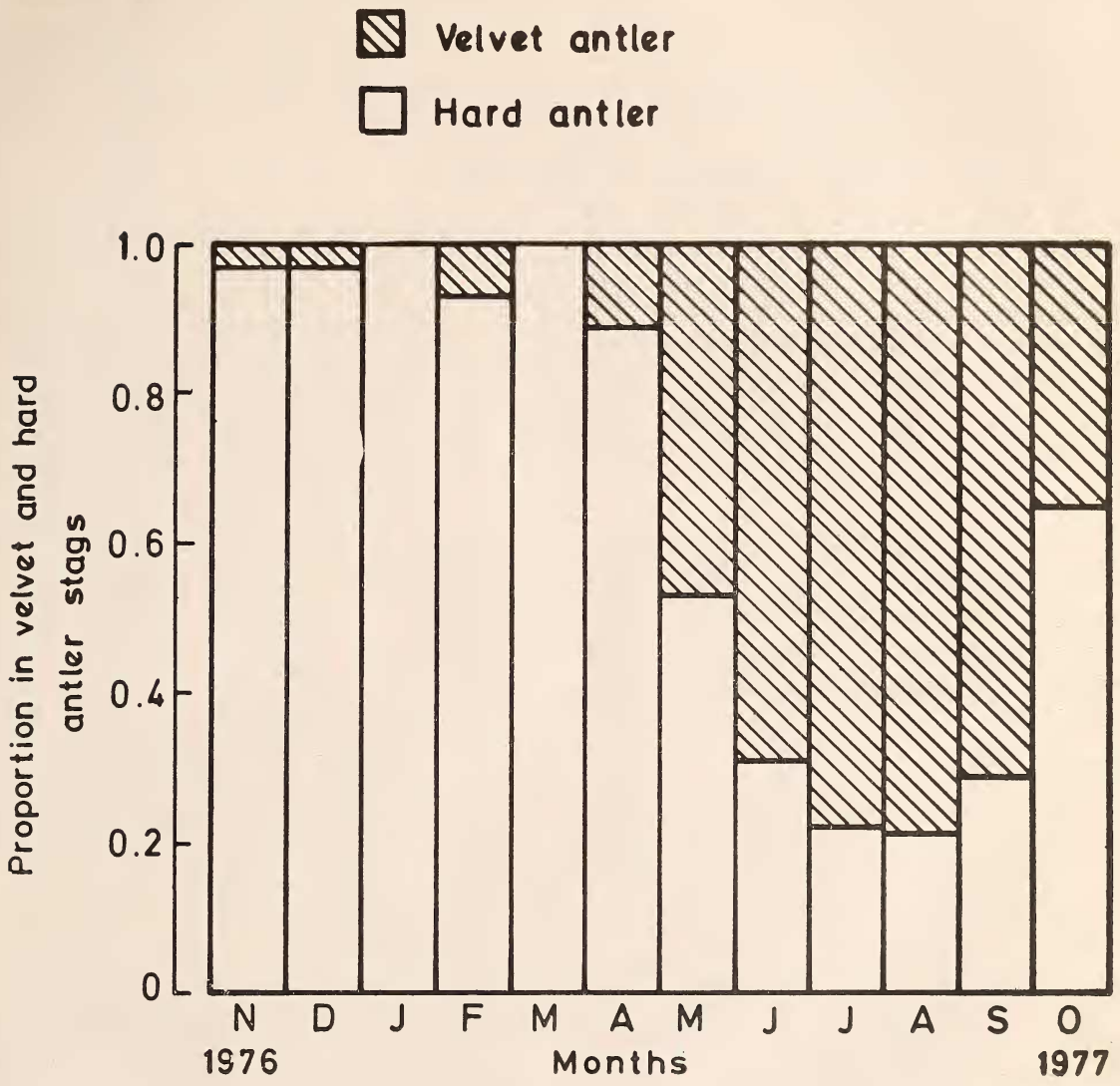


Fig. 10. The proportion of sambar stags in velvet and hard antlers.

and Padhi (1972) there were 14 ♂♂ and 21 ♀♀ or a ratio of 2:3. The null hypothesis that ♂ and ♀ sex ratio was even is acceptable ($Z = 1.645$, $P > .05$). Nevertheless the sex ratio showed a bias in favour of ♀♀ throughout the year (Table 4). Average ♂ to ♀ ratio during November, December and January was 41:100. Schaller sexed 11 kills and found the ratio of ♂ and ♀ to be 120:100 and ratio in the population was 30:100. Male kills were more common than expected ($X^2 = 11.46$, d.f., 1, $P < .005$). My data (see discussion: predation and sex of prey) and Schaller's confirm preferential predation on yearling and adult ♂♂.

Rut

In Bandipur sexual activity was indicated by antler development, sore patch, wallowing and courtship behaviour. Stags in hard antlers were observed mainly between November and April and most ♂♂ had shed their antlers by May (Fig. 10).

Fawning period

Sambar fawn population is difficult to estimate because they do not consistently follow the ♀♀ during the first 3 months (Eisenberg and Lockhart 1972). Lone resting fawns were flushed out of cover on 24 occasions (January, February and June each 3, March 4, April 5, May and August each 2 and November and December each once). This does not coincide with the beginning of rut (November) and may be the result of young fawns freezing in cover instead of running away when approached. Forty one kills of young sambar fawns (38 by dhole, 2 by leopard and 1 by tiger, Fig. 11) show that more fawns were killed from August to March than expected ($X^2 = 11.2$, d.f., 1, $P < 0.001$) which assuming an 8 month gestation period (Acharjyo and Misra 1971) indicated these fawns were conceived during the rutting season, November to April. Fawn to doe ratio averaged for May, June and July 1977 was 32:100 and for the same period in 1978 the ratio was 41:100.

Mortality

The major cause of observed mortality was predation. Of the 379 kills found in this study sambar accounted for 17%. Sambar remains were found in 14% of dhole ($n = 509$) and leopard scats ($n = 70$) and 31% of tiger scats ($n = 36$). Predation took a heavy toll of sambar fawns. Of the 66 sambar kills 41 (62%) were of fawns < 4 months of age. An examination of 93 predator scats with sambar remains (72 of dhole, 11 of tiger and 10 of leopard) showed 71 of them (76%) had sambar fawn remains. I removed 5 snares set for sambar.

Antipredator behaviour

Sambar have an excellent sense of smell but like chital they seem unable to distinguish immobile objects. Sambar have the ability to sense danger from the excitement created by the presence of a predator (hunt 3). The sambar's preference for dense cover may be an adaptation against dholes but could be disadvantageous when stalked either by tiger or leopard. Sambar do not have any white markings on their bodies which may be a cryptic adaptation for a life in the scrub. Sambar antipredator behaviour include:

(a) Watching: Schaller (1967) mentions the ability of sambar to remain motionless for long periods of time. This was observed many times and may enable them to remain unseen while investigating the movement of predators;

(b) Investigation of curious objects: When wind was not in their favour sambar were curious to know the identity of the object which

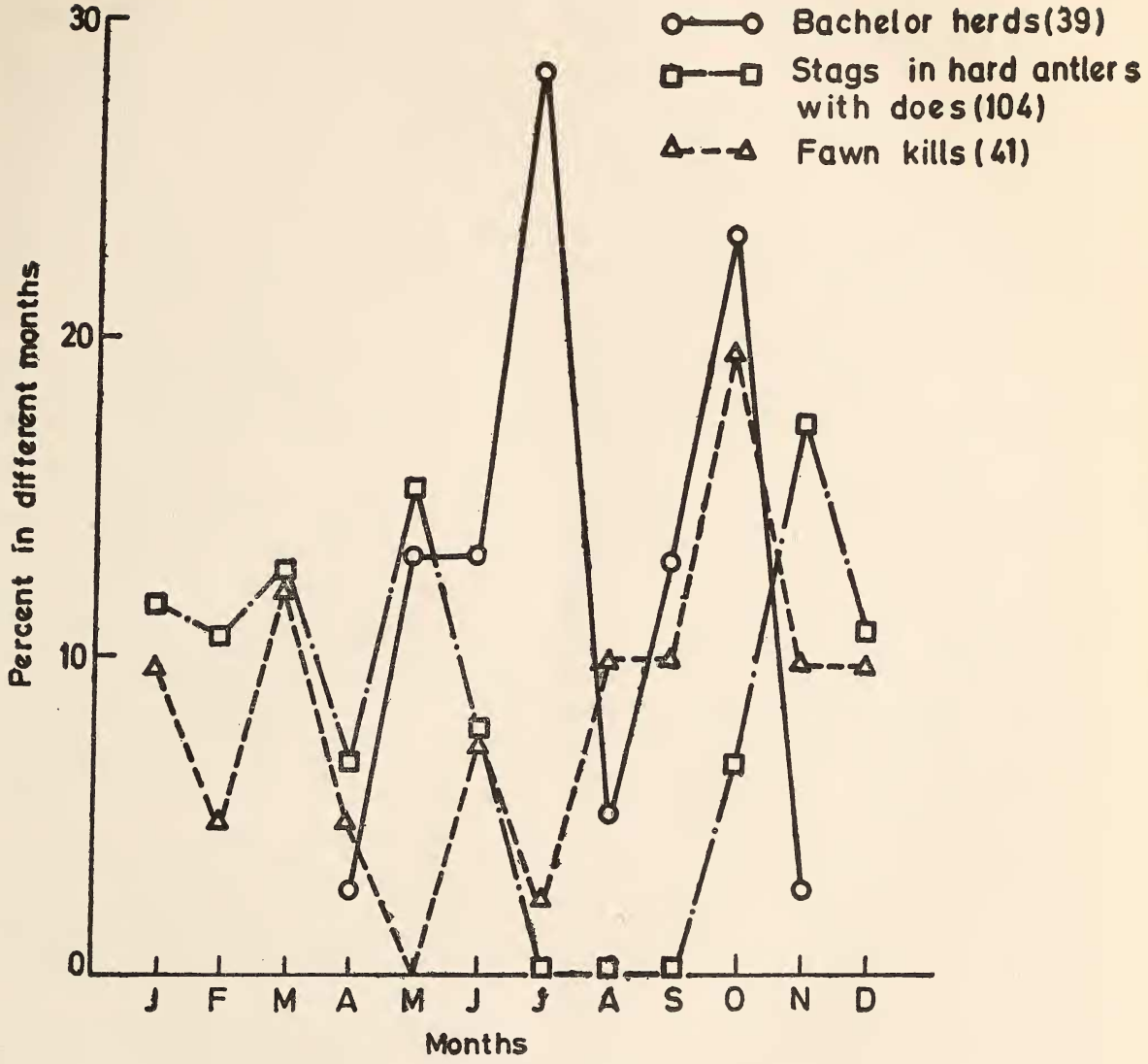


Fig. 11. Bachelor herds of sambar, stags in hard antlers with does and fawn kills seen over the period August 1976 to July 1978

attracted their attention. Once a sambar mistook me for a predator and keeping the tail vertical, thumping forelegs and jerking the head it approached me 7 to 10 m. A solitary adult tusker interrupted the observation. This type of curious approach may be advantageous if the stalking predator is forced to launch a preemptive attack;

(c) Belling: Sambar called when they saw predators including jungle cat. Their alarm calls varied in tone and intensity depending on the type of predator and whether or not it was hunting. When hunted by dholes sambar with young were not observed to call but adults without young did (hunt 6). When dholes hunted, ♀ ♀ with fawns were seen to leave the area (hunt 3). A leopard going through a scrub prompted a sambar to call in a subdued tone but the sambar did not run. Once 2 tigers killed a sambar doe in a patch of scrub and their movements were indicated by sambar alarms from the same scrub. It appeared that for the 2 days the tigers remained in the scrub the sambar of that area were not unduly disturbed. But on 6 different occasions when a tiger was hunting in the same scrub 1 to 14 sambar emerged giving alarm calls. Probably on these occasions the tiger was hunting;

(d) Remaining motionless in cover: Brander (1927) noted that sambar squat like a hare so they would be passed undetected. Once a fawn and another time a stag stayed in cover allthrough aware of my approach. The fawn placed its chin on the ground and lay crouched until I passed 5 m of it. The stag remained motionless until I was within 8 m;

(e) Seeking refuge in water: This was the most common and successful strategy against dholes and was seen 15 times. On 6 occasions sambar ran over a 3 m high tank bund to get into water. On 2 occasions they ran through scrub to get into 6 to 7 m wide puddle. While in the water sambar seemed to have control over the situation. Together an adult and a yearling doe successfully kept off the study pack from a fawn (hunt 21). While in water sambar kept their rumps together as moose (*Alces alces*) do (Mech 1966) (hunts 20 and 21). They also rose on their hind feet and struck at dholes with forefeet (hunt 20). The fear of being chased again often forced sambar to stay in water even after the dholes left (hunt 21). In Bandipur dholes did not press home their attack when sambar retreated to water (hunt 21) as chital were the main prey species;

(f) Attack: On land sambar were not able to protect their fawns successfully from dholes (hunts 5, 16, 17 and 19). But on 3 occasions in open areas adult sambar chased dholes — on two occasions solitary does chased 3 to 5 dholes and another time 2 does, watched by 2 yearling does, drove off 3 dholes (e.g., hunt 19). When sambar faced dholes on land they bristled their body hair, held their tails vertical laid back the pinnae and exposed the white of the eyes. Snorting was also heard. While approaching dholes they kept the head low to the ground extended the neck and stamped their forefeet.

On two occasions sambar fawns screamed when chased by dholes even though not physically assaulted (hunt 20 and 21). When chased by dholes sambar did not enter Bandipur village as was done by chital on 6 occasions.

Ecological adaptations of breeding in chital and sambar

Continued optimal season is seen in tropics and equatorial regions where the seasons vary so little that young may be born at any time of the year and have an approximately equal chance of survival (Sadleir 1969). Although Bandipur is a tropical monsoon forest its envi-

ronment has seasonality in food availability which presents a situation some what similar to the 'fixed optimal season found in temperate areas' (Sadleir 1969).

In Bandipur food for ungulates was scarce and was of low nutritional value from January to April. Grass was tender and green from May to August. Chital fawns, however, were born even in very dry months. Although chital fawns nibble grass when they are a week old they begin eating it in quantity by 5 weeks (Graf and Nicholas 1966). By the time many chital fawns were weaned and had greater food requirements the fodder condition had dramatically improved which enabled them to feed exclusively on grass.

A continued supply of tender grass from May to August would also enhance the development of the embryo conceived at the end of April. Further more the arrival of the north east monsoon by the end of September and the sprouting of more grass in October may provide the embryo with all essential nutrients. Thus at Bandipur chital are finely adapted to their environment by evolving weaning and pregnancy to synchronize with the time of abundant growth of grass.

In sambar rut commenced after the end of the May to September aggregation. Assemblage before the rut could lead to the formation of new breeding herds, social order and exchange of gene pool. Sambar hinds conceiving between November end and the beginning of May may have nutritional difficulties. The ability of sambar to eat a wide spectrum of forage, however, may nullify this hardship. Sambar fawns born in dry months have thin vegetation cover but their ability to remain hidden may help them overcome this difficulty.

Wild Pig

There were 155 sightings of sounders and solitary ♂♂. Lone ♂♂ were seen 81 times (53%) and the largest group had 32 (8 adults and 24 young). Of the 155 sightings 123 (79%) were seen in wet and cool months and 32 (21%) during the dry season. Pigs may be mostly nocturnal in their activity during the dry months.

The estimated number of pigs in the core area in July 1977 was 50 animals, a density of 2.5/Km². Stripers (young piglets) were seen in the months of June, July and August which implies littering after rains in May.

Wild pigs were the major terrestrial scavengers of the area. Five times they were seen eating the kill remains of dhole; three times in the presence of the pack (Johnsingh 1978). A chital fawn killed by a leopard and a chital doe killed by a tiger were also scavenged.

Table 7

Frequency of occurrence of food items in 509 dhole scats collected in Bandipur

Food Item	No. of scats with the remains of	Percent	No. of times with the remains of	Percent
Chital adult	126	24.75	127	23.87
Chital fawn	138	27.11	143	26.88
Hare	71	13.95	74	13.91
Sambar adult	16	3.14	18	3.38
Sambar fawn	54	10.6	54	10.15
Microtine Rodents	31	6.09	34	6.39
Cattle	14	2.75	14	2.63
Muntjac	8	1.57	8	1.50
Langur	6	1.18	6	1.13
Wild pig	4	0.79	5	0.94
Gaur calf	1	0.2	1	0.19
Beetle	5	0.98	13	2.44
Grass	35	6.88	35	6.58
Total	509	100	532	100

TABLE 8

SIGHTINGS OF WILD PIG, GAUR* AND MUNTJAC CORRELATED WITH RAINFALL

	Jan.	Feb.	March	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.
Wild Pig	7	4	8	9	27	17	28	16	14	10	11	4
Gaur	1	0	0	0	9	7	6	11	9	3	1	1
Muntjac	9	9	18	17	0	1	4	7	7	4	2	8
Average of the 3 years' rainfall	0	15.95	20.2	143.18	100.41	88.82	192.55	175.12	252.4	218.3	136.85	5.4

* sightings of groups and solitary bulls.

Daniel (1967) suggests that pigs may kill and eat fawns but this was not observed during this study.

Only 5 pig kills were collected. Four of these were adult boars killed by tigers and one was an unsexed adult killed by dholes. This latter pig had attempted to escape the dholes by backing into a pit and facing the dholes. Pig remains were seen in 6% of tiger scats (Fig. 12) and 1% of dhole scats (Table 7).

GAUR

Gaur was one of the most common large mammals of Bandipur before the 1968 rinder pest epidemic. During the study there were 48 sightings of gaur; lone bulls were seen 25 times (52%). The largest herd consisted of 45 to 60 animals. It was not possible to classify the animals with regard to sex except that mature bulls were black and females and young bulls were brown. Six herds were classified and within these there were 19 black adults (22%), 43 brown adults (51%) and 23 young (27%). There is a positive correlation (+569) between the number of sightings of gaur and rainfall (Table 8). Nearly 96% of gaur sightings were in wet and cool months.

MUNTJAC

This deer was not seen close to human habitation and its habitat was more often shared by sambar than by chital. In total 86 animals were seen belonging to 66 groups. Six animals could not be sexed. The rest were classified as 25 ♂♂ (31%), 39 ♀♀ (49%) and 16 young (20%). The sex ratio was 64 ♂♂ : 100 ♀♀. Of the 66 groups solitary animals were seen 50 times (76%) groups of 2 12 times (18%) and groups of 3 or 4 4 times (6%).

TABLE 9

GROUP SIZE OF ELEPHANTS COUNTED IN THE CORE AREA — AUGUST 1976 — JULY 1977

	August	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July
Total groups seen	12	23	25	18	27	18	15	6	7	19	24	35
Av. group size	5.9	9.8	12.5	7	8.7	8.5	6.05	6.8	6.3	5.78	7.87	9.7
Range	4–10	2–36	2–29	2–37	2–26	2–28	2–14	3–9	3–11	2–11	2–39	2–14

Muntjac showed a distinct movement pattern in relation to rain. Sixty one (71%) animals were seen during dry months when water was restricted to certain ponds. An estimate of 20 animals for the core area gave a density of 1 animal/Km².

No muntjac kill was collected ; 3% of leopard, 3% of tiger and 2% of dhole scats had muntjac remains in them.

Porcupine

Tracks and droppings of porcupine were commonly seen. The estimate for the core area was 100 animals, a density of 5/Km². Signs indicated that they centered their activities around water holes in summer. Six per cent of tiger and 1% of leopard scats had porcupine remains.

Hare and Rodents

The number of black naped hare was assessed to be 200 animals for the core area or a density of 10/Km². Fourteen per cent of dhole, 11% of leopard, 10% of jungle cat and 3% of tiger scats had hare remains. Crested Hawk Eagles were seen eating hare three times and once a hare, to escape the aerial attacks of a Crested Serpent Eagle (*Spilornis cheela*), abruptly crouched 3 times. Rodents were found in 64% of jungle cat, 14% of leopard and 6% of dhole scats.

Elephants

Elephant was not a common prey animal but its contribution to the biomass was significant. During the first year 2283 sightings were classified: adult tuskers 18%, juvenile tuskers 11%, Cows 40%, juvenile cows 17% and calves 15%. Mean group size between November and April varied between 6 and 8.7 and for May

to October it was between 5.8 and 12.5 (Table 9). During the wet and cool season there were nearly 100 elephants in the core area and for the dry season the estimate was around 20. One calf was killed and eaten by a tiger. A leopard was chased by an adult tusker and dholes were chased 8 times.

Peafowl

This potential prey was restricted to the core area and there were nearly 180 birds. The sex ratio in the population was biased in favour of males throughout the year. In April, a month prior to the active breeding season, the ratio was 224 ♂♂ : 100 ♀♀. This can be compared with the ratio of 47 ♂♂ : 100 ♀♀ at Injar (Johnsingh and Murali 1980).

Peahens lay 3 to 5 eggs (Ali 1972) and in Bandipur chick mortality was high. Of the 27 broods seen 8% had 1 chick, 48% 2 chicks, 22% 3, 19% 4 and 4% had 5. Five kills (2 ♂♂ with trains, 1 ♂ without, 1 ♀ and 1 chick) were collected. Crested Hawk Eagles killed all 3 ♂♂ and a jungle cat killed the chick. Many brooding females killed in the scrub may go unnoticed.

Antipredator behaviour of Prey Species

The response of the prey species to the predator depends on the activities of the predator. If the predator is not hunting and happens to go past the prey the latter becomes alert, curious, and subdued alarm calls may be produced. When the predator is hunting the response entirely changes and any one of the following strategies — hiding in cover, flight or attack may be adopted. In general the antipredator behaviour is influenced by the size, habitat, sex, reproductive condition, sociability of the prey and size of the predator. Eisenberg and Mckay (1974) give a detailed sequence of events and their alternatives which may be followed by a terrestrial herbivore upon perceiving a predator. Table 10 summarizes the various antipredator behaviours seen in Bandipur. Certain antipredator behaviour are discussed further.

Bunching

Gregarious behaviour is a form of cover seeking in which an animal tries to reduce its chance of being caught by a predator (Hamilton 1971). Bunching of chital in the presence of dhole was first reported by Sharatchandra and Gadgil (1975). Reproductive investment of chital ♂♂ (sperms) is insignificant when compared with those of ♀♀ which carry the embryo for 8 months and nurse the fawn for 3 to 4 months. This high reproductive investment may prompt the ♀♀ to come forward and investigate the danger while the ♂♂ run to the safety of the middle of the herd. Bunching was seen in truly social mammals such as wild pig, gaur and elephants.

Remaining motionless in cover

This is an excellent means of escape for small animals and was often shown by hare and occasionally by chital. Sweeny *et al.* (1971) observed this in white tailed deer (*Odocoileus virginianus*) when chased by dog (*Canis familiaris*) and call this behaviour 'holding'. Older black-tailed stag (*Odocoileus hemionus*) remain bedded to escape hunters (Dasmann and Taber 1956). Interestingly this behaviour was shown by the much larger sambar. If sambar remains bedded when a predator approaches the bush down wind there is every chance the deer, whose dark brown coat blends well with the dim interior of the scrub, may escape unnoticed.

TABLE 10

ANTIPREDATOR BEHAVIOUR SEEN IN BANDIPUR

Species	Preferred habitat	Watching	Curiosity attraction	Bunching	Alarm Call	Distraction display	Tail flashing	Flight	Distress Call in flight	Abrupt crouching while running	Staying motionless in cover	Abrupt dispersion	Startling call	Deposition of pedal gland secretion	Seeking refuge in water	Attack
Hare	Scrub short grass	+	?	—	?	?	+	+	+	+	+	—	—	—	—	—
Muntjac	Forests with dense under growth	+	+	—	+	?	+	+	+	?	+	—	—	?	—	+
Chital	Scrub – short grass ecotone	+	+	+	+	+	+	+	+	?	+	+	+	+	+	—
Sambar	Scrub forest, tall grass	+	+	+	+	+	—	+	+	—	+	+	+	?	+	+
Wild pig	Scrub forest and short grass with water	+	+	+	Grunt	—	—	+	+	—	—	+	+	?	—	+
Gaur	Forest, grass land	+	+	+	Snort	—	—	+	—	—	—	—	—	—	—	+
Elephant	Scrub forest, grass land	+	+	+	?	—	—	+	—	—	—	—	—	—	—	+

+ = Present; — = Absent; ? = Unknown.

Alarm calls

Kin selection (Hamilton 1964, Maynard Smith 1965) and individual selection (Trivers 1971) have been evoked as two explanations for the evolution of alarm calls. Yahner (1980) discusses the functions and adaptiveness of barking in muntjac. Alarm calls of chital in the presence of a stalking predator may be a 'pursuit invitation signal' (Smythe 1977). Though chital form social groups late prenatal and early post natal care of the young rests only with the individual does and in that type of situation alarm calls may have evolved through individual selection. This is more so in sambar.

Through direct and indirect evidence many a time I recorded chital calling in the presence of leopard and tiger but never I saw chital calling when they clearly saw dholes. A stalking predator could be dangerous only at close quarters and repeated alarms could be given while the distance between them is sufficiently large for a reasonable chance for chital's escape if the stalking predator is hunting. This may not be the case with dholes. When dholes ran through the scrub chital gave subdued single alarms. Presumably the deer did not identify the predator.

Seeking refuge in water

Burton (1940) suggested that water is not a place of refuge and the habit of animals running to water or being killed near water is the result of their down hill race which accidentally takes them to water. Observations in Bandipur indicate that sambar purposely ran to water. A study of 9 kills including those of 5 adults (e.g., hunt 3) showed that certain prerequisites are necessary for this tactic to be successful:

(a) Water should be shallow enough to allow sambar to use forelegs powerfully;
(b) Water should not be too shallow which would permit dholes to walk in and attack;
(c) It would be better for sambar if there is scrub bordering the edge of water not affording space for the intercepting dholes.

Attacks

Wild pig, sambar, gaur and elephant actively chased dholes. Muntjac are said to attack and kill domestic dogs *Canis familiaris* (Hoogerwerf 1970). If the size of the prey determines the capability to attack then chital which are larger than muntjac and wild pig should attack. Horns and tusks evolved primarily as the weapons for the fight between the members of the same species rather than as defence against predators (Geist 1966). Chital is another example for this speculation. Probably shorter weapons like the canines of muntjac and pig can be effectively used against a predator than a longer antler. Sheer size of gaur and elephants enable them to intimidate dholes. Observations of sambar does and gaur cows chasing dholes in the presence of their young support the hypothesis that 'chasing predators may give naive prey individuals the opportunity to learn to recognize predators by participating in low risk chases' (Kruuk 1972, Berger 1979).

Biomass

For understanding the effect of predation a calculation of biomass is necessary. The first attempt to estimate the biomass in the oriental region was made by Schaller and Spillett (1966) for the Keoladeo Ghana Sanctuary. Recently Eisenberg and Seidensticker (1976) reviewed the data on ungulate communities and their biomass in the Indian subcontinent.

In Bandipur if the contribution of other small

Leopard was the second common predator in Bandipur.

A young tiger in Bandipur
(Photos: *Author*)

Jackal was rare in the study area.

Sambar-dhole interaction.
(Photos: *Author*)

prey species such as porcupine ($8 \times 100 = 800$ Kg.), hare ($2 \times 200 = 400$ Kg.) and peafowl ($3 \times 180 = 540$ Kg.) was added to the figure derived in Table 6 the biomass of prey animals was between (68,825 + 1740) 70,565 Kg. and (73,587 + 1740) 75327 Kg. or 3528 Kg. to 3766 Kg/Km². The average was 3647 Kg/Km². With the contribution of elephants the biomass ranged between 289,765 and 294,527 Kg. or 14,488 to 14,726 Kg/Km². The average was 14,607 Kg/Km².

This biomass was maintained almost throughout the wet and cool season. During the dry season owing to the dispersal of chital and sambar and the absence of gaur the prey biomass went down to 2863 Kg/Km². The prey biomass for dry months ($2863 \times 5 = 14{,}315$) and for wet and cool seasons ($3647 \times 7 = 25{,}525$) gave an average of 3,320 Kg/Km² for the year. In dry season hardly 20 elephants remained in the core area and their biomass (2,192 Kg/Km² with prey biomass 2,863 Kg/Km²) gave 5055 Kg/Km² which was 35% of the average biomass of the wet and cool season (14,607 Kg/Km²).

Another aspect of the study of biomass concerns the relative proportions contributed by the different species in the community (Mckay and Eisenberg 1974). In the core area during the wet and cool season numerically less and highly mobile elephants formed 76% of the total biomass, chital 11% and sambar 9%. The prey biomass of the core area is much higher than the biomass of 465 Kg/Km² for the entire Reserve (calculated from Wesley 1977). Major reasons for the core area having a high prey biomass were evenly distributed water holes and heterogeneous vegetation which afforded forage, escape cover and rest and fawning sites.

PREDATORS

Number and Densities

In the core area there was a pack of dholes varying in number between 7 and 18 giving a density between 0.35 and 0.9 dholes/Km². Mean number of adults was 8.3; when pups were present the mean number was 16. Dholes were the major predators and accounted for 80% of the kills (n = 379). Two or 3 leopards and at least a ♂ and a ♀ tiger hunted in the core area. Leopards accounted for 15% of the kills and tigers for 5%.

Hunting Habits of Dholes

Time of hunt

The exact time was recorded for 124 kills made in the morning. Of these 96 (77%) were made after sunrise and 28 (23%) before sunrise. Of 67 kills in the evening 52 (78%) were seen before sunset and 15 (22%) after sunset. Three kills were made at different nights (e.g., hunt 11) of which 2 nights were moonlit.

Prelude to hunt

When prelude to the hunt was observed (4 instances) the dholes rested and played on roads and on 3 occasions near their defecation sites. While resting close to one another they nuzzled and rubbed their bodies together. Active submission, tail wagging, chase and ambush were common. Mounting was noted once. On 3 occasions some dholes playfully walked on branches of fallen trees. Once this peaceful get together suddenly gave way to vigorous play which abruptly subsided as the pack started off to hunt. Vocalization at the climax of play, reported in *Lycaon* (Estes and Goddard 1967) and in wolves (Mech 1970) was not heard.

At the beginning of the hunt dholes often moved in single file and the trotting speed was

around 9 km/hr. Occasionally one or two dholes lagged behind sniffing a tuft of grass, lapping water or scavenging a bone.

Locating prey

Dholes have an excellent sense of smell and were able to locate the observer more than 100 m away (hunt 12). Dholes located prey by sight but they also depended on smell (hunts 3, 4, 8 and 12). In scrub where visibility was limited they primarily depended on smell. When the prey ran sight and hearing aided them to follow the quarry. Running sounds of prey in the scrub informed other dholes of the progress of the hunt. In one case 6 or 7 dholes approached a herd of gaur by stalking through the tall grass.

Dholes adopted two hunting strategies. In one strategy they moved through the scrub in an extended line formation (e.g., hunts 5, 8, 16, 18, 19 and 24) and any adult may begin the attack when it locates prey. In the other strategy some pack members remained at the periphery of the scrub to intercept fleeing prey as it was flushed (e.g., hunts 1 to 5, 15 and 19). Both formations are effective for locating hidden fawns and resting adults. Dholes adopted the former strategy 39 times and the latter 14 times in total.

Rush and chase

Other than gaur, wild pig and occasional sambar all prey ran when chased by dholes. Handicapped prey trailed behind (e.g., hunt 6). Dholes may determine vulnerability by the prey's initial reaction. During the early phase of the chase dholes run faster than the prey. Owing to this and team work most of the chases did not last long. In 92% of 48 occasions the chase ended within 500 m of its starting point. Twice the chase went beyond 500 m (e.g., hunt 1) and on two occasions the distance could not be assessed.

One widely prevalent belief is dholes hunt in relays pursuing prey casually at a loping canter until the quarry is exhausted (Burton 1940, Davidar 1975, Krishnan 1975b). In a dense habitat especially where many animal tracks crisscross it would be difficult for dholes to run in relays or follow a prospective prey animal for a long distance. Even in the African plains *Lycaon* hunt occasionally in brief relays (Kruuk and Turner 1967, Schaller 1972) but Estes and Goddard (1967) never saw a true relay chase.

Attack and kill

Small mammals like hare and chital fawn were seized by any part of the body as they ran. With a single head shake such small prey were killed instantly (e.g., hunts 8 and 14). Dholes were capable of inflicting serious wounds on the rump and flanks of the larger prey (hunts 5 and 6) and consequently even large chital stags were brought down (e.g., hunt 10).

Generally larger animals are attacked from behind and the usual points of attack are rump and flank. Dholes are wary if prey are capable of injuring either with antlers or forelegs (hunt 9). The nose hold seen in wolves (Mech 1970) and *Lycaon* (Estes and Goddard 1967, Van Lawick 1971, Schaller 1972, Malcolm and Van Lawick 1975) was used by dholes when the speed of the prey was arrested. Nose holding enabled dholes to accelerate their attack on the rump and flank which ultimately subdued the victim. If the prey's nose is caught while it stands in water the weight of the dhole may drown the prey before the dhole frees itself from suffocation. This was interpreted as intentional drowning of the prey by dholes (Sankhala 1977). However, I cannot believe

that dholes drown their prey intentionally. Once the nose hold was used to drag a chital fawn out of water (hunt 13).

During this study 27 out of 40 fresh kills had snout injury (4 sambar ♂♂, 6 chital stags in velvet, 15 chital stags in hard antlers, 1 chital doe and 1 sambar fawn). Snout injury occurred in all sambar males, in 55% of chital stags in velvet and in 82% of chital stags in hard antler. More chital stags in hard antler were injured on the snout by nose hold than expected (Hypergeometric distribution, p. 0878, $p > .05$).

Attack on the rump and flanks led to evisceration. Bite wounds, shock and loss of blood eventually killed the prey. Of 40 fresh kills checked none had throat wounds. Dholes removed the scrotum during hindquarter attack and this has led to the popular belief that they deliberately emasculate their prey. The scrotum was usually eaten as it was found on only 4 occasions ($n = 33$).

Prejudice against dholes arises from their method of disemboweling prey and eating them alive (hunts 3 and 9). Ten direct observations showed that prey weighing 50 Kg or less were killed within 2 minutes after the attack began. The maximum time was 15 minutes (hunt 9). Killing was delayed by human interference as 'some members of the pack hung back apprehensively and were not able to do their share in killing' (Van Lawick 1971). In the absence of human interference a yearling ♂ sambar was killed within 7 minutes by the pack of 15 (hunt 3).

Dholes do not deserve the reputation as cruel hunters as their method and time required to kill are not much different from those of other predators. Hyenas take 1 to 13 min. (Av. = 6.3) to kill wild beast (Kruuk 1972). A lioness took more than 8 min. to kill a warthog and 3 lionesses more than 7 min. to kill a zebra (Schaller 1972). Tigers (Burton 1925) and lions (Schaller 1972) have been reported to eat their prey alive. Obviously natural selection has led to effective means of disabling prey (incapacitation) rather than quick and painless death.

When the pack moves through the scrub there may be opportunities to attack 2 or 3 large prey animals. There was only one incident of dholes, however, killing 2 large chital stags at one time. This suggests dholes are not wanton killers. Kills were not made by a particular dhole (see hunts 1, 6, 10, 11 and 13).

Sequence of eating a carcass

Dholes fed excitedly soon after killing. The belief that every dhole gets its share was not true when kills were small (e.g., hunt 1). Even for medium sized animals like chital doe and sambar fawn, especially when the undivided pack was around, there was always squabbling until the excitement of the hunt was over. Fawns were torn to pieces within seconds after killing and each dhole ran away with its share (e.g., hunt 8). Even when the kill was as large as a yearling sambar or an adult chital stag all pack members did not lie around the kill and eat. When my presence was noted they dragged the kill away (e.g., hunts 2, 5, 12 and 17) and once a male weighing nearly 18 kg dragged a 49 kg chital doe for 5 m through grass and creepers.

As all dholes could not eat at the rump they tugged at the carcass from all directions. Belly and loin were soon torn open and the entrails were pulled out. The viscera were dragged aside (hunts 3, 9, 13 and 24). If it was a fawn the intestine was eaten spilling the contents. The rumen was usually left though its tissue was some times eaten. Lungs were often torn out but were not always eaten. There was always a scramble for the liver and the heart.

Dholes seemed to relish the eye balls. Of the 40 fresh kills checked 21 had both eyes remov-

ed, in 8 cases left and in 6 cases right eye were removed. Five animals had intact eyes. In 4 hunts dholes removed the eye balls as soon as the kill was made. Pinnae were also eaten. Of the 40 kills both the pinnae were removed in 17 animals, left pinnae in 12 and right in 5. In 16 cases pinnae were present. Uneaten dismembered pinna was (three times) found close to kills.

When a kill was fully eaten dismembered parts of the prey were left around the kill site. Usually the vertebral column with the attached ribs and the skull formed the main piece. The limb bones and pectoral girdle were usually separated. If the prey was large the skin was neatly removed of meat and then left with the head attached. When dholes ate a mature chital stag (around 75 kg) the remains weighed around 25 kg. (33%). However, on 4 occasions the remains varied between 51 and 68% (Av. = 55). Dholes left these kills in the absence of human disturbance. This contradicts the belief that dholes leave only bone fragments even from large kills such as adult sambar.

Feeding dholes frequently drank if water was nearby. If water was some distance away they headed for the nearest waterhole soon after eating. When the day became hot before the kill was eaten dholes did not go to their distant rest sites. Instead they found shelter under dense thickets near the kill till the evening.

Speed of eating and meat consumption rate

As Kruuk (1972) noted in hyena competition between feeding dholes expressed itself mostly in the speed of eating rather than in fighting. Dholes consumed their kills quickly. The pack (9 adults + 9 pups) once ate 50 kg of meat from a 70 to 75 kg chital stag within 90 min. They were aware of my presence and had a brief uninvited interaction with 4 village dogs. Another time 8 adults and 7 pups ate 14 kg of meat from a yearling chital doe (30 to 35 kg) within 4 min.

For three periods I collected almost all the kills made by the pack (Table 11). The prey varied from chital fawn to chital stag, number of dholes ranged from 15 to 18 and the meat available per dhole varied between 0. 7 kg and 3 kg. The total meat consumed by a dhole during the 15 day period was 27.9 kg (1.86 kg of meat per day or 0.103 kg of meat per kg of 18 kg dhole). This is comparable to the consumption rates for wolves (2.6 to 6.3 kg per wolf per day or 0.09 to 0.19 kg per kg., Mech 1966) and for *Lycaon* (2.0 to 4.0 kg per *Lycaon* per day or 0.11 to 0.15 kg per kg, Estes and Goddard 1967). The estimate for the dhole may be a little lower than the actual amount of meat eaten as they may be feeding on smaller animals which would go unrecorded. My observations indicate that when dholes ate about 2 kg in the morning they did not hunt in the evening. On 7 occasions when the morning kill provided each dhole < 2 kg of meat they hunted again in the evening. On 6 occasions when the first kill was a fawn one more kill was made in the same hunting session.

Scavenging and attendant scavengers

Dholes scavenged once on a tiger kill (Johnsingh 1979b) and 7 times on leopard kills. Dholes returned and ate their own kills for the second time either on the same day or 2 or 3 days after ($n = 11$). Although dholes were not seen hunting langurs remains of langurs were seen in 6 dhole scats. This may have been the result of scavenging. Food caching was not observed though it is seen in wolves (Murie 1944) and rarely in *Lycaon* (Malcolm 1980).

The jungle crow was the major scavenger at Bandipur. Besides this there were King Vultures (*Torgos calvus*), Whitebacked (*Gyps bengalensis*), Longbilled (*Gyps indicus*), Pariah

Dholes at a sambar kill.

Sambar skin removed of meat by Dholes.
(Photos: *Author*)

Dholes at a chital stag kill. Jungle Crows are in the foreground.
(Photo: *Author*)

TABLE 11

ESTIMATION OF MEAT CONSUMPTION RATE OF DHOLE

S.No.	Date and time	Particulars of prey	Estimated weight (in Kg.)	Weight of remains (in Kg.)	No. of dholes	Average meat available per dhole (in Kg.)
1.	7 Sept. '77 morning	Chital stag velvet age class V	70–75	30	16 or 17	2.5
2.	8 Sept. '77 evening	Chital doe age class VIII	50	10	„	2.5
3.	9 Sept. '77 < 0600	Chital doe age class VI	50	9	„	2.5
4.	10 Sept. '77 1800	Chital stag hard 88 cm, age class V	75	30	„	3
5.	11 Sept. '77 0730	Big chital fawn	30	6	„	1.5
6.	11 April '78 0830	Chital fawn	20	2	18	1
7.	12 April '78 0600	Chital fawn	15	1.5	18	0.7
8.	13 April '78 0610	Chital stag velvet, age class VI	75	21	18	3
9.	14 April '78 < 0600	Chital doe, age class VIII	50	12	18	2
10.	15 April '78 1830	Chital stag velvet, age class VI	70–75	24	18	2.5
11.	16 April '78 1900	Sambar fawn	30	3	18	1.5
12.	15 June '78 0800	Chital yearling doe age class II	30	5	15 or 16	1.7
13.	16 June '78 0630	Chital fawn	15	1.5	„	0.8
14.	17 June '78 1100	Chital fawn	25	3	8 adults 7 pups	1.5
15.	18 June '78 1400	Chital fawn	20	2	„	1.2

Kites (*Milvus migrans*) and on one occasion a White Scavenger Vulture (*Neophron percnopterus*). Village dogs scavenged on dhole kill remains four times.

OBSERVATIONS ON OTHER PREDATORS

Tiger

There were 18 sightings. The tigress of the area was followed by 2 cubs from the end of May 1977. Sightings of the 3 till March 1978 indicated that the tigress was successful in rearing the cubs.

Once when I mimicked the whistle of a dhole, suspecting the presence of a predator in the scrub, a tiger came out growling and stood at the edge of the scrub with pinnae laid flat. I

TABLE 12

FREQUENCY OF OCCURRENCE OF FOOD ITEMS IN 67 JUNGLE CAT SCATS COLLECTED IN BANDIPUR

Food item	Frequency of occurrence	
	No. of scats	Per cent
Rat and mouse	43	64.17
Bird remains	9	13.43
Hare	7	10.45
Lizard	5	7.46
Chital fawn	3	4.48

3 scats had grass — 2 in combination with rat remains and 1 with bird remains.
9 scats had insect remains — 7 along with rat remains, 1 with bird remains and 1 with hare remains.

mimicked dhole whistle another time when a tiger left a waterhole. The tiger turned back came forward two steps and then sat and looked for 2 minutes in my direction.

Sloth bear

There were 16 sightings but tracks and droppings showed that sloth bear were not rare. During April 1977 when water was restricted to the perennial ponds tracks showed that 3 adults and 1 young made use of the core area.

Of the 95 scats analysed over the period August 1976 to July 1977 one had bones and hairs of hare and another a beetle wing. Forty nine had earth, termites and ants probably of the genus (*Componotus* spp.); 35 had earth and fruit, 4 earth and grass and 5 earth and beeswax. *Cassia fistula* seeds were seen in December, March, April and May; *Zizyphus jujuba* fruits in January; *Cordia myxa* and *Syzygium cumini* in June and July. These findings are similar to those of Laurie and Seidensticker (1977).

Jungle cat

There were 28 sightings; 14 were in September and October. Results of the scat analysis are presented in Table 12. One dead jungle cat was seen and cause of death could not be ascertained as crows had mutilated the carcass.

Jackal and others

There were 13 sightings of jackals 5 of which were of pairs. Eleven sightings were in dry months.

Stripe-necked mongoose were seen 8 times hunting for small animals along pond margins.

Python was seen 5 times and once a python killed a chital fawn.

Crested Hawk Eagle was the most common avian predator of hare and peafowl.

KILLS LOCATED

In the core area 233 chital, 56 sambar, 1 wild pig, 3 hare and 2 cattle calves, all killed

TABLE 13

COLLECTED KILLS OF DHOLES, LEOPARD AND TIGER IN BANDIPUR (AUGUST 1976 — JULY 1978)

	Chital*			Sambar			Wild	Hare	Langur	Cattle	Ele-	Village	Dhole	Leo-
	Fawn	♀	♂	Fawn	♀	♂	Pig				phant	Dog		pard
Dhole	100	68	64	46	3	7	1	3	—	3	—	—	—	—
Leopard	11	18	9	2	—	1	—	—	1	10	—	5	1	—
Tiger	1	3	1	1	5	1	4	—	—	1	1	—	—	1

* Seven chital kills by dholes could not be aged and sexed.

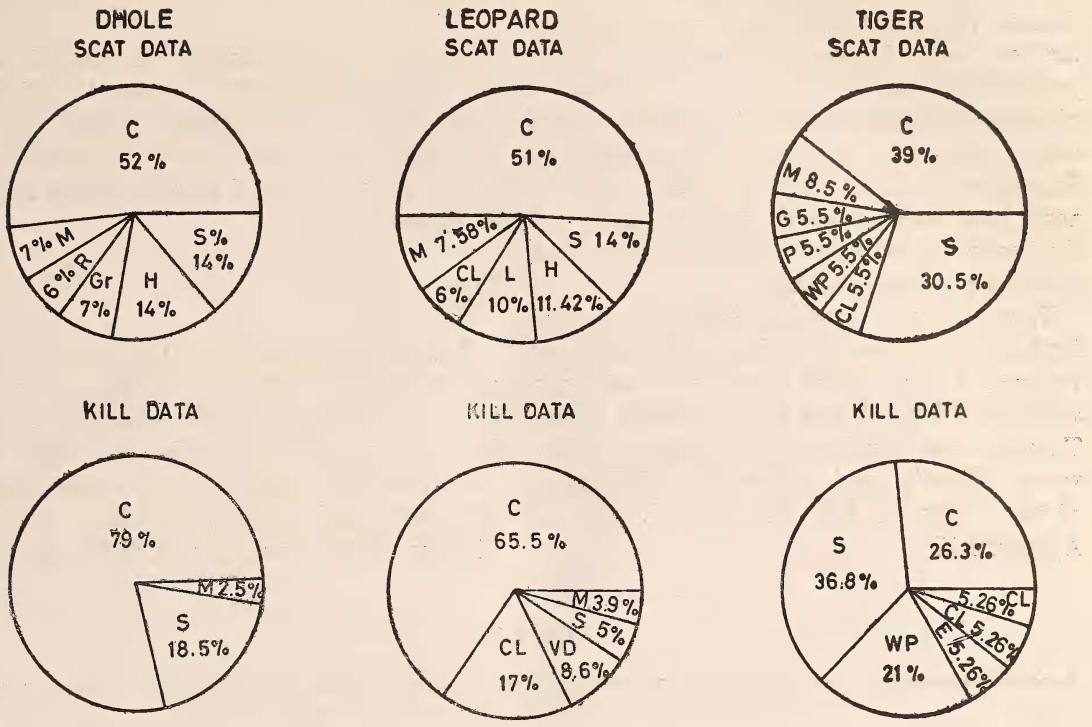


FIG. 12. FOOD ITEMS OF DHOLE, LEOPARD AND TIGER AS SHOWN BY SCAT AND KILL DATA. C: CHITAL, S: SAMBAR, H: HARE, WP: WILD PIG, R: RODENTS, CL: CATTLE, P: PORCUPINE G: GAUR, Gr: GRASS, VD : VILLAGE DOG, LC : LEOPAPD CUB, E: ELEPHANT CALF, M : MISCELLANEOUS.

by dholes, were collected. Outside the core area 6 chital and 1 cattle calf kills of dholes were seen. In total 302 dhole kills were seen (Table 13 and Fig. 12).

Of the 58 kills by leopard (Table 13 and Fig. 12) 66% was chital and 5% sambar. Inability to collect sambar fawns killed by leopard may be due to their occurrence in the scrub. Ten cattle and 5 village dogs were also killed by leopard.

A classification of tiger kills (n = 19) is shown in Table 13 and Fig. 11. Chital and sambar fawn kills of tiger are well represented in scats (Fig. 12) but 1 chital and 1 sambar fawn killed by tiger were collected. This is mostly due to tiger's ability to consume more than 20 kg of meat in one night and to dispose of small kills within hours.

Scat Data

Dhole

Of the 509 scats 24 had remains of more than one animal species. Chital was the most common prey eaten (Table 7, Fig. 12) followed by hare and sambar. Although only 3 cattle calves were killed by dholes 14 dhole scats had cattle remains. Nearly 500 cattle were driven

through the Reserve to the slaughter houses in Kerala. Weak and unfit cattle abandoned on the road were frequently killed by the local people and leopard. Scavenging on the remains of these cattle may account for 14 dhole scats having had cattle remains. In the months of September and October, after the onset of north east monsoon, partly chewed remains of the beetle (*Dorysthenes rostratus*) were found with other animal remains.

Thirty five scats consisted almost entirely of fresh grass. On two occasions grass was seen wrapped around chital fawn hoof and bone splinters of hare. A scat had 5 *Lantana* leaves, *Themeda* and *Cymbopogon* spp grass, 3 tape worms (*Taenia* spp.) and mucous. Estimation of the number of kills from scats is given in Appendix II.

Leopard

Results of the analysis of leopard scats (n = 70) are presented in Figure 12. Of these chital formed 51%, sambar 14% and the rest was composed of cattle, langur and hare. Calculation of the number of kills from scats is given in Appendix II.

Tiger

Results of the analysis of tiger scats (n = 36) are presented in Figure 12. Three scats contained soil along with the remains of chital fawn (1 scat) and porcupine (2 scats). Two scats (one with sambar fawn remains and the other with cattle remains) had large quantities of grass. Thirty nine per cent of the scats con-

TABLE 14

A CORRELATION OF SCAT AND KILL DATA TO ESTIMATE THE EXPECTED KILLS AND BIOMASS OF WILD PREY REMOVED FROM THE FOCAL AREA BY THE DHOLES

Prey species and their weight (in Kg.) used in computation		No. of meals the pack (13 animals) can have	No. of scat samples with the remains of	Corrected estimate of scat	Observed Kills	Expected Kills	Corrected estimate of Kills	Biomass of corrected estimate of kills (in Kg.)
*Adult and yearling sambar	(110)	2	18	21	10	9.5–12	11	1210
Sambar fawn	(32)	1	54	63	46	54	63	2016
**Chital adult				148	134	131	153	9098
(♂ : 69; ♀ : 44)		1	127					
Chital fawn	(15)	0.5	143	167	98	286	334	5010
Muntjac	(15)	0.5	8	9	—	16	18	270
Wild pig	(30)	1	5	6	1	5	6	180
Hare	(2)	0.08	74	86	3	222	258	516
Gaur calf	(50)	1	1	1	..	1	1	50
Rodent	(0.1)	0.004	34	40	..	8160	9600	960
							Total ..	19310

*Average weight, derived from actual weights, is used in computation.

**Biomass of corrected estimate of kills was calculated based on the sex ratio seen in the kill (94♂ : 100♀).

TABLE 15

CORRELATION OF SCAT AND KILL DATA OF THE LEOPARD

Prey species and their weight used in computation (in Kg.)	No. of meals a leopard can have	No. of scat samples with the remains of	Probable occurrence of scats with 95% confidence interval		Corrected estimate of scats		Observed Kill	Expected Kill	Biomass (in Kg.)
			Lower Limit 1%	Upper Limit 8%	5 Lower Limit	5 Upper Limit			
Yearling sambar (130)	4	2					1	1	130
Sambar fawn (32)	2	8			6	40	2	3–20	640
*Chital adult ♂ : 69, ♀ : 44	3	10			9	50	27	3–17	1413
Chital fawn (15)	1.5	27			24	135	11	16–90	1350
Muntjac (15)	1.5	2			2	10	—	1–5	75
Hare (2)	0.33	8			6	40	—	18–120	240
Langur (8)	1	7			6	35	1	6–35	280
Porcupine (8)	1	1			1	5	—	1–5	40
Rat (0.1)	0.01	1			1	5	—	100–500	50
Total ..		66**							4218***

* Biomass is calculated for the kill observed. (9♂ : 18♀)
** Excluding 4 scats with cattle remains.
*** Biomass of 10 cattle and 5 village dog kills is not included.

tained chital, 31% sambar and the rest was composed of cattle, pig and gaur remains.

DISCUSSION

In this report I have presented observations on the large mammalian prey predators in the core area of my study in Bandipur. While dholes were primarily diurnal, tiger and leopard were essentially nocturnal. All the three predators chiefly preyed on chital and sambar and the local people derived their animal protein stealing chital and sambar kills. The basic questions that are to be answered to fully understand the interactions among the prey, predators and local people are as follows :

a) What was the prey-predator ratio?

b) What ecological and behavioural features isolated the predators in the core area?

c) What ecological conditions permitted the co-existence of predators?

d) What was the effect of predation on chital and sambar population? and

e) What was the impact of people stealing chital and sambar killed by predators?

The answers to the last two questions are presented in Appendix III and IV.

PREY-PREDATOR RATIO

From the scat data it was inferred that dholes killed 19,310 kg (Table 14), leopard 4,218 kg

(Table 15) and tiger 3203 kg including the elephant calf (Table 16) of prey biomass in the core area. This was nearly 20% of the 66,400 kg (average biomass was 3,320 kg/Km² and the core area was 20 Km²), the average total biomass calculated for the core area. This serious predation is probably because of the sudden removal of 100 + cattle from the study area at the onset of the study. Inspite of this heavy predation there was a significant increase in chital and sambar population (Appendix III and IV).

Average predator biomass 534 kg (13 dholes = 234 kg; tiger = 180 kg, 2 leopards = 120 kg) and prey biomass showed a ratio of 1:124. In Ngorongoro Crater the ratio was 1:100 and in Serengeti 1:250-300 (Schaller 1972).

Ecological Separation of Predators

When several predatory species hunt in the same area competition in the sense of joint demand for a limited prey resource is likely to occur. One way in which such competition can be reduced is for the predators to occupy different habitats or to use the same one at different times (Schaller 1972). Table 17 lists 15

Table 16

Correlation of scat and kill data of tiger

Prey species and their weight used in computation (in Kg.)	No. of meals a tiger can have	No. of scat samples with the remains of	Probable occurrence of scats with 95% confidence interval		Corrected estimate of scats	Observed Kill	Expected Kill	Biomass of expected kill (in Kg.)
			Lower Limit 1%	Upper Limit 22%				
Sambar adult (200)	4	2			22 Lower Limit 3 Upper Limit 63	6	6	1200
Sambar fawn (32)	1.5	9			27	567	1	18–378	576
*Chital adult ♂ : 69; ♀ : 44	2	6			18	378	4	9–189	446
Chital fawn (15)	1	8			24	504	1	24–504	360
Muntjac (15)	1	1			3	63	—	3–63	45
**Wild Boar (50)	2	2			6	126	4	3–63	200
Gaur Calf (50)	2	2			6	126	—	6–63	150
Hare (2)	0.15	1			3	63	—	1–9	2
Porcupine (8)	0.5	2			6	126	—	3–63	24
Total ...		33***							3003****

* Sex ratio in the kill was 1♂ : 3♀.

** Biomass is calculated for the observed kills.

*** One more scat with grass and earth was collected.

**** If the elephant calf weight is added the biomass reaches 3203 Kg.

mechanisms that reduce competition between Bandipur predators.

Differential use of habitat

Signs of predators were seen in 138 quadrats of the core area (n = 219). Hard terrain and tall grass were the major reasons for not recording predator occurrence in other quadrats. Of the 138, indications of all the 3 predators were seen in 31 (23%). Evidence for dhole alone were seen in 35 (25%) and such figures for leopard and tiger were 13 and 7 respectively. Thirty seven quadrats (27%) contained sign of dhole and leopard. Dhole and tiger signs and clue to tiger and leopard occurrence were seen in 9 and 6 quadrats respectively. This suggests possible 'tolerance' (mutual use of space) between dhole and leopard and 'intolerance' between leopard and tiger. This 'intolerance' led to a tiger killing and eating a leopard cub (Johnsingh 1979a) and 'tolerance' resulted in a leopard killing a dhole pup. Schaller (1967) and Seidensticker (1976a) report avoidance between tiger and leopard.

Large cats like the tiger (Schaller 1967, Sunquist 1981) and the lion (Wright 1960) rarely kill prey on short grass or open habitats. In areas north east of Bandipur, where vegetation was thin, 56 quadrats were checked for predator signs. Dhole, leopard and tiger signs were found in 21, 13 and 2 quadrats respectively. Fifty six quadrats in dense vegetation, south west of Bandipur, yielded 47, 39 and 28 quadrats with signs of dhole, leopard and tiger respectively. This indicates preference of tiger for dense vegetation.

TABLE 17

ECOLOGICAL DIFFERENCES AND BEHAVIOURAL SEPARATION BETWEEN PREDATORS

Ecological and behavioural parameters	Tiger	Leopard	Dhole
Nocturnal ..	+	+	—
Diurnal ..	—	—	+
Need for cover ..	+	+	—
Tolerance for sun ..	—	+	—
Need for water ..	+	—	+
Tolerance for human disturbance ..	0	—	—
Arboreal ..	—	+	0
Smallest mammal killed (scat analysis) ..	Hare	Rat	Rat
Largest wild mammal killed ..	Elephant calf	Sambar yearling stag	Adult sambar doe
Food caching ..	+	+	0
Scavenging ..	+	+	+
Tolerance for rain ..	+	—	+
Sociability ..	Solitary	Solitary	Social, lives in packs
Territory marking ..	+	+	+
Intraspecific/ Interpack tolerance ..	—	—	?

+ Yes, Great; – Less; 0 Absent.

All 19 kills by the tiger and 55 of the leopard (n = 58) were found in scrub. Sixty three per cent of fresh kills of dholes (n = 219) were in scrub, 17% in meadows, 9% on or near roads, 8% in or near water and the rest in tree jungle and near stream beds. Dholes like leopards and tigers, entirely do not require cover for killing prey.

Prey size

All three predators were capable of killing large prey but in tiger kills the > 100 kg class formed 42% (Table 18). Larger species must

TABLE 18

WEIGHT CLASSES OF KILLS OF THE TIGER, LEOPARD AND THE DHOLE

Weight class in Kg.	<25	25-50	50-100	>100
Tiger — kills	2	8	1	8
Percent in total kills	10.5	42.1	5.26	42.1
Leopard — kills	18	22	9	9 (1 Sambar + 8 cattle)
Percent in total kills	31	37.9	15.5	15.5
Dhole — kills	127	96	75	4
Percent in total kills	42	31.78	24.8	1.3

rely upon energy source that occur in large food items unless they can collect smaller prey with great efficiency (McNab 1963) and carnivores usually prey upon herbivores of about their own size and weight (Bourliere 1963). Excluding 8 adult cattle kills 69% of leopard kills weighed < 50 kg. Kruuk and Turner (1967), Pienaar (1969) and Schaller (1972) have recorded that leopards very rarely kill prey heavier than 100 kg. Of the dhole kills the > 100 kg class formed 1%, 50 to 100 kg group 25%, 25 to 50 kg group 32% and < 25 kg class 42%.

No evidence of leopard killing wild pig was seen in Bandipur which was frequently observed in Wilpattu (Eisenberg and Lockhart 1972) and in Chitawan (Seidensticker 1976a). Dholes also very rarely killed wild pig. On the contrary tiger killed 4 adult boars which formed 21% of their total kills. When chital, an easier prey to kill, are abundant leopard and dhole may not risk attacking either a solitary boar which may be difficult to kill or a member of the sounder which can trigger off the protective instinct of the sounder. The ability of the tiger to hunt prey ranging from hare to elephant calf indicates that tigers use a much wider spectrum of food resources.

Prey density and utilization by predators

In July 1977 the total number of prey animals in the core area (excluding porcupine, hare and peafowl) was 1247 to 1310. Of this chital constituted 69%. Kill data show that chital formed 79, 66 and 26% respectively of the prey of dholes leopard and tiger. Fifty two per cent of dhole, 51% of leopard and 39% of tiger scats had chital remains (Fig. 12). Fewer chital remains in the scats of dholes is due to the occurrence of the remnants of hare and rodents in scats which are not included in the total number of prey (1247-1310). It is also due to the scavenging by the dholes on cattle and langur which are poorly represented in kill data. The same situation lowers the occurrence of chital remains in the scats of leopard.

Tiger scat and kill data reveal that proportionately fewer chital were killed than were present in the population. This can be attributed to the antipredator behaviour of chital which assemble in the campus and in open areas to spend the night where they are immune to tiger predation. More over, prefer-

ence of chital for areas around Bandipur, where tiger may not be able to hunt in day time, keeps a major fraction of the population free from tiger predation.

Sambar were only one fifth as abundant as chital. Yet tiger proportionately preyed more on sambar (Fig. 12). Sambar use the scrub intensively, live in small groups and do not rest in open areas. These ecological and behavioural factors make the less abundant sambar more vulnerable to tiger predation or tiger may specifically hunt sambar.

Predation and sex of prey

Males are said to be more susceptible to predation. Weakened condition after rut (Hornocker 1970) and territorial contest (Estes and Goddard 1967, Schaller 1972) make ♂♂ vulnerable to predation. During this study 132 yearling and adult chital killed by dholes were collected. The ratio in the kill was 94 ♂♂ : 100 ♀♀ and in the population it was 84 ♂♂ : 100 ♀♀. Predation of ♂♂ was not significantly different from expected.

Dholes very often killed stags with long antlers (Figs. 13 and 14, Table 19). Two hypotheses could be offered for stags with long antlers being vulnerable to predation:

a) Stags with long hard antlers which take an active part in rut (Sharatchandra and

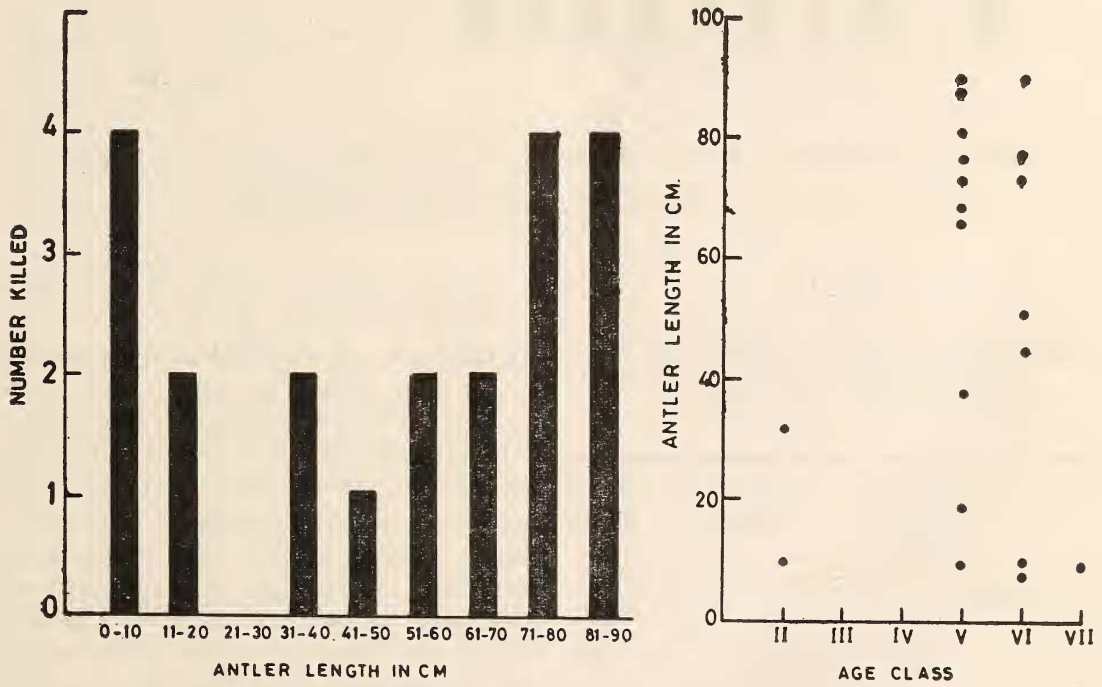


Fig. 13. Antler length and age classes of 20 chital stags in velvet killed by dholes; 3 animals in shed antlers are included in 0-10 category (August 1976 to July 1978).

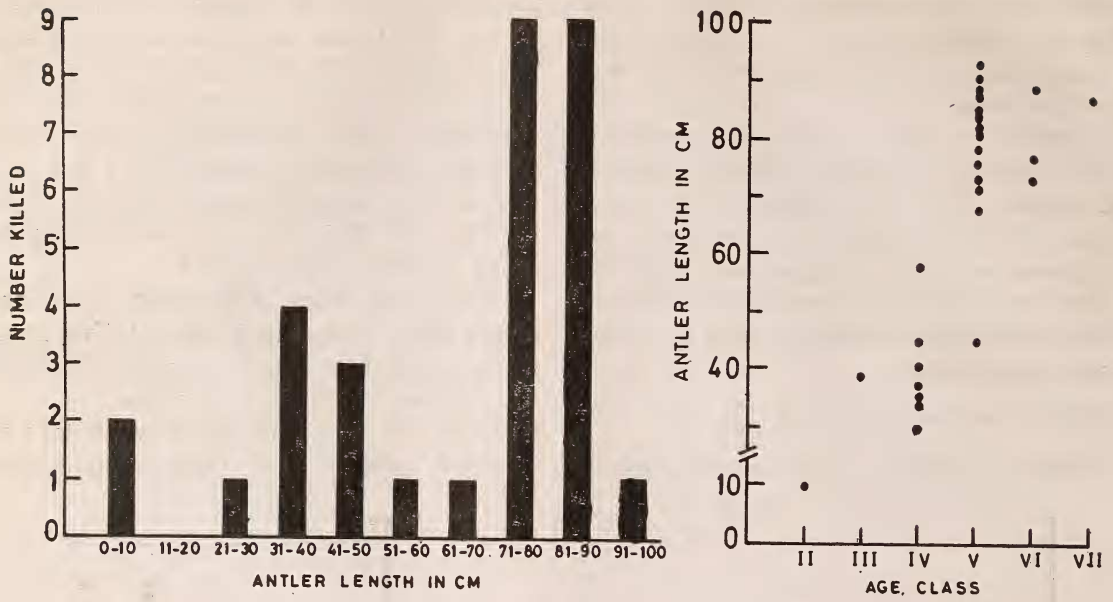


Fig. 14. Antler length and age classes of 31 chital stags in hard antlers killed by dholes (August 1976 to July 1978).

TABLE 19

HARD ANTLER LENGTHS OF CHITAL ♂♂ FROM THE POPULATION AND FROM DHOLE KILLS AUGUST 1976-JULY 1978 — BANDIPUR

	Stags with < 25 cm. antlers	25–50 cm antlers	> 50 cm antlers
Random sample from the population (n = 77)	26	27	24
Kills (n = 31)	1	8	22

Preference to kill stags with longer antlers was significantly greater than expected.
$X^2 = 15.6$, d.f., 1, $P < .001$.

Gadgil 1980) are indifferent to predators and are spent after the rut;

b) there is strong sexual selection among males for large antlers but there is also counter selection by predators against large antlers.

Number of chital stags in hard antlers killed by dholes in different months (Table 20) did not indicate any significant concentration during or after rut. Nor any significance was seen when the kill data were compared with chital stags in hard antlers in the population (Table 21). Hence the first hypothesis is rejected. The explanation for the second hypothesis is that stags with large antlers may be hampered when running through dense vegetation and are easily killed.

During fawning does frequently visit scrub which may make them more vulnerable to tiger

TABLE 20

NUMBER OF CHITAL STAGS KILLED BY DHOLES IN DIFFERENT MONTHS (AUGUST 1976 TO JULY 1978)

	J	F	M	A	M	J	J	A	S	O	N	D	Total
Stags in hard antlers	—	—	4	3	4	3	6	3	3	4	4	—	34
Stags in velvet antlers	3	3	4	8	3	—	1	2	2	1	1	2	30

TABLE 21

CHITAL STAGS IN HARD ANTLERS KILLED BY DHOLES AUGUST 1976-JULY 1978, BANDIPUR

	Stags counted	Kills	Kills collected for equal # of stags
May to October	1897	23	8.24
November to April	680	11	11

Preference to kill stags from May to October (rutting season) was not significantly greater than expected.
$X^2 = 0.4$, d.f., 1, $P > .05$.

TABLE 22

RELATING CHITAL KILLS WITH PROBABLE NUMBER OF SCATS PRODUCED

	Chital fully eaten	Chital eaten more than once	Chital stolen after some feeding	Chital stolen before any feeding	Kills of leopard scavenged	Total
Kills	113	7	6	8	4	138
Probable number of scats produced	113	14	3	0	4	134

and leopard predation. Tiger Kills (1 ♂ + 4 ♀ ♀) and leopard kills (9 ♂ ♂ + 18 ♀ ♀) had more does than stags; however, even leopard predation of does was not significantly more common than expected ($X^2 = .463$, d.f., 1, $P > .5$).

Sex ratio in the sambar population was 41 ♂ ♂ : 100 ♀ ♀ and in dhole kills the ratio was 233 ♂ ♂ : 100 ♀ ♀ (n = 10). Dholes killed more males than expected ($X^2 = 11.95$, d.f., 1, $P < .005$). All males killed were yearlings or young adults which suggests that their solitary habits may have made them prone to dhole predation.

Predation and age of prey

Chital of the age class II, III and IV because of their agility and alertness may escape dholes but often fall prey to leopards which hunt by stealth and surprise. Chital belonging to the above mentioned classes formed 25% and 37% of the total yearling and adults killed by the dholes (n = 131) and leopard (n = 27) respectively. Forty three per cent of chital killed by dholes (n = 231) were fawns and the corresponding figure for leopard was 23% (n = 38). The inability of dholes to kill more yearling and young adult chital is similar to coyote predation where deer between 2 and 6 yrs. of age appear most secure from coyote caused mortality (Ogle 1971). Similarly wolf predation is heaviest on fawns and old animals (Murie 1944, Mech 1966, Pimlott *et al.* 1969, Kolenosky 1972).

Yearling females of age class II and III were much more susceptible to dhole predation (19% of ♀ kills, n = 67) than yearling males (6% of ♂ kills, n = 64). The probable reason was pregnancy.

Caching food

Dholes did not cache food and this may result from the absence of any significant remains from a meal. Tiger and leopard usually cached the kill when it was large enough to afford more than one meal. Curiously leopards in Bandipur had left 6 chital kills, all < 50 kg, in open and a hind leg of only one chital was covered with litter and earth. The leopard carries its kill up a tree when potential food thieves are about (Ewer 1973). In Chitawan leopards pulled about half of their kills up trees (Seidensticker 1976a) and in Wilpattu kills were kept in trees to keep them safe from hunting packs of jackals (Eisenberg and Lockhart 1972). In Bandipur in spite of the frequent scavenging by dholes and human beings leopards hauled their kills up trees only three times.

Ecological conditions permitting the co-existence of Predators

Large prey biomass, a large proportion of ungulate biomass in the smaller size classes and dense vegetation structure enabled tigers and leopard coexist in Chitawan (Seidensticker 1976a). The prey biomass of the core area (3320 kg/Km²) is higher than the 2400-2500 kg/Km² of wild and domestic prey biomass of Kanha (Schaller 1967) and 766 kg/Km² of Wilpattu (Eisenberg and Lockhart 1972) and the 2789 kg/Km² of Chitawan (Seidensticker 1976b). As in Chitawan in the core area there were not many species of ungulates in the small size classes and chital alone formed 69% of prey number or 48% of large hoofed mammal biomass. The heterogeneous habitat of the core area with many stream beds may be much more ideal for the predators and the prey species than the tall grass/riverine forest of Chitawan and the open short grass meadow/ *Shorea* forest habitat of Kanha.

Complexity of vegetation types, high prey biomass and a large number of chital as the optimum prey for dhole and leopard and a sizable population of sambar and wild pig for the tiger allowed these predators to coexist in the core area. An analysis of the factors mentioned in Table 17 shows that the first 12 parameters could determine the survival of the three predators. A predator which can survive in a deteriorating habitat should be both nocturnal and diurnal and should have the ability to feed on small and large prey. Further the capacity to cache food, climb trees and scavenge would also promote survival. Hence leopards would survive in a much disturbed habitat where dholes would be rare and tigers totally absent.

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References

Acharjyo, L. N. and Misra, R. (1971): Age of sexual maturity of three species of wild animals in captivity. *J. Bombay nat. Hist. Soc. 68*: 446.

——— and Padhi, G. S. (1972): Some observations on distributions of Zoo births among common wild mammals. ibid. *69*: 175-178.

Ali, S. (1972): The book of Indian birds. Bombay Natural History Society, Bombay.

Berger, J. (1979): Predator harassment as a defensive strategy in Ungulates. *Amer. Midland. Nat. 102*: 197-199.

Berwick, S. (1976): The Gir forest: An endangered ecosystem. *Am. Sc. 64*: 28-40.

Bourliere, F. (1963): Specific feeding habits of African carnivores. *Afr. Wildl. 17*: 21-27.

Brander, A. D. (1927): Wild animals in central India. Edward Arnold Co., London.

Burton, R. W. (1925): Panther and wild dogs. *J. Bombay. nat. Hist. Soc. 30*: 910-911.

———(1940): The Indian wild dogs. ibid. *41*: 691-715.

Crandall, L. (1964): The management of wild mammals in Captivity. University of Chicago Press, Chicago.

Daniel, J. C. (1967): The Point Calimere Sanctuary. *J. Bombay nat. Hist. Soc. 64*: 512-523.

Dasmann, R. F. and Taber, R. (1956): Behaviour of Columbian black tailed deer with reference to population ecology. *J. Mammal. 37*: 143-64.

Davidar, E. R. C. (1975): Ecology and behaviour of the dhole or Indian wild dog (*Cuon alpinus* Pallas). *In*: Fox, M. W. (Ed.), The Wild canids, Van Nostrand Reinhold, New York.

Eisenberg, J. F. and Lockhart, M. C. (1972): An ecological reconnaissance of Wilpattu National Park, Ceylon. *Smithsonian contrib. Zool. 101*: 1-118.

Eisenberg, J. F. and McKay, G. (1974): Comparison of ungulate adaptations in the New World and Old World tropical forests with special reference to Ceylon and the rain forests of Central America. *In*: The behaviour of ungulates and its relation to management. (V. Geist and F. Walther, eds.) Vol. 2: 585-602. International union for Conservation of Nature and Natural Resources, Morges, Switzerland.

——— and Seidensticker, J. (1976): Ungulates in Southern Asia: A consideration of biomass estimates for selected habitats. *Biol. Conserv. 10*: 294-308.

Estes, R. D. and Goddard, J. (1967): Prey selection and hunting behaviour of the African wild dog. *J. Wildl. mgmt. 31*: 52-70.

Ewer, R. F. (1973): The Carnivores. Cornell university press, Ithaca, New York.

Floyd, T. J., Mech, L. D., and Jordan, P. A. (1978): Relating wolf scat content to prey consumed. *J. Wildl. mgmt. 42*: 528-532.

Fox, M. W. and Johnsingh, A. J. T. (1975): Hunting and feeding in wild dog. *J. Bombay nat. Hist. Soc. 72*: 321-326.

Geist, V. (1966): The evolution of horn like organs. *Behaviour, 27*: 175-214.

Graf, W. and Nicholas, L. (1966): The Axis deer in Hawaii. *J. Bombay nat. Hist. Soc. 63*: 629-734.

Hamilton, W. D. (1964): The genetical evolution of social behaviour. *J. Theor. Biol. 7*: 1-52.

——— (1971): Geometry for the selfish herd. *J. Theor. Biol. 31*: 295-311.

Hoogerwerf, A. (1970): Udjungkulon, the land of the last Jawan rhinoceros. E. J. Brill, Leiden.

Hornocker, M. (1970): An analysis of mountain lion predation upon mule deer and elk in Idaho primitive Area. Wildl. Monogr. 21, The wildlife Society, Washington, D.C.

Johnsingh, A. J. T. (1978): A wild boar (*Sus scrofa*) sharing wild dog's (*Cuon alpinus*) kill. *J. Bombay nat. Hist. Soc. 75*: 211-212.

——————— (1979a): Evidence for a tiger eating a panther cub. ibid. *76*: 152-153.

——————— (1979b): An instance of wild dogs scavenging on a tiger's kill. ibid. *76*: 360-361.

——————— AND MURALI, S. (1980): The ecology and behaviour of the Indian peafowl (*Pavo cristatus*) of Injar. ibid. *75* (Supplement): 1069-1079.

JOSLIN, P. (1973): Factors associated with decline of the Asiatic lion. *In*: R. L. Eaton (Ed.), The World's cats, *1*: 127-141.

KOLENOSKY, G. B. (1972): Wolf predation on wintering deer in East central Ontario. *J. Wildl. mgmt. 36*: 357-369.

KOPPIKAR, B. R. AND SABNIS, J. H. (1976): Identification of hairs of some Indian mammals. *J. Bombay nat. Hist. Soc. 73*: 5-20; *74*: 50-59.

KRISHNAN, M. (1975a): A guide to the tourism zone of the Bandipur Tiger Reserve, Karnataka.

——————— (1975b): India's wildlife in 1959-70. Bombay Natural History Society, Bombay.

KRUUK, H. (1972): The spotted hyena. University of Chicago Press, Chicago.

——————— AND TURNER, M. (1967): Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa, *Mammalia. 31*: 1-27.

LAURIE, A. AND SEIDENSTICKER, J. C. (1977): Behavioral ecology of the sloth bear (*Melursus ursinus*). *J. Zool. Lond. 182*: 187-204.

MALCOLM, J. R. (1980): Food caching by African wild dogs (*Lycaon pictus*). *J. Mammal. 61*: 743-744.

——————— AND VAN LAWICK, BARON (1975): Notes on wild dogs *Lycaon pictus* hunting Zebras. *Mammalia. 39*: 231-240.

MAYNARD SMITH, J. (1965): The evolution of alarm calls. *Amer. Natur. 99*: 59-63.

McDOGUAL, C. (1977): The face of the tiger. Rivington books, London.

MCKAY, G. M. AND EISENBERG, J. F. (1974): Movement patterns and habitat utilization of ungulates in Ceylon. *In*: The behaviour of ungulates and its relation to management. (V. Geist and F. Walther, eds.) Vol. 2: 708-721. International union for conservation of Nature and Natural Resources, Morges, Switzerland.

MCNAB, B. K. (1963): Bioenergetics and the determination of home range size. *Am. nat. 97*: 133-140.

MECH, L. D. (1966): The wolves of Isle Royale. U. S. Natl. Park. Serv. Fauna Ser. 7, Washington.

——————— (1970): The wolf: The ecology and behaviour of an endangered species. Double day, New York.

MUCKENHIRN, N. A. AND EISENBERG, J. F. (1973): Home ranges and predation of the Ceylon leopard. *In* R. L. Eaton (Ed.), The world's cats. *1*: 142-175.

MURIE, A. (1944): The wolves of Mount Mckinley. U. S. Natl. Park. Serv. Fauna Ser. 7, Washington.

NEGINHAL, S. B. (1974): Project Tiger Management plan of the Bandipur Tiger Reserve. Karnataka State.

OGLE, T. (1971): Predator-prey relationships between coyotes and white tailed deer. *North. West. Sci. 45*: 213-218.

PANWAR, H. S. (1979): Population dynamics and land tenures of tigers in Kanha National Park. Paper presented at International symposium on the tiger, February 22 and 23, 1979, New Delhi, India.

PIENAAR, U. DE (1969): Predator-prey relations amongst the large mammals of the Kruger National Park. *Koedoe. 12*: 108-76.

PIMLOTT, D. H., SHANNON, J. A. AND KOLENOSKY, G. B. (1969): The ecology of the timber wolf in Algonguin Park, Ont. Dept. Lands. For. 90 pp.

PRATER, S. H. (1971): The book of Indian animals. Bombay Natural History Society, Bombay.

SADLEIR, R.M.F.S. (1969): The ecology of reproduction in wild and domestic mammals. Methuen and Co., London.

SANKHALA, K. (1977): Tiger: The story of the Indian tiger. Simon and Schuster, New York.

SCHALLER, G. B. (1967): The deer and the tiger: A study of wildlife in India. University of Chicago Press, Chicago.

——————— (1972): The Serengeti Lion. The University of Chicago Press, Chicago.

SCHALLER, G. B. AND SPILLETT, J. (1966): The status of big game species in the Keoladeo Ghana Sanctuary, Rajasthan. *Cheetal 8*: 12-16.

SEIDENSTICKER, J. (1976a): On the ecological separation between tigers and leopards. *Biotropica. 8*: 225-234.

——————— (1976b): Ungulate populations in Chitawan valley, Nepal. *Biol. Conser. 10*: 183-210.

SHARATCHANDRA, H. C. AND GADGIL, M. (1975): A year of Bandipur. *J. Bombay. nat. Hist. Soc. 72*: 625-647.

——————— (1980): On the time — budget of different life history stages of chital *Axis axis*. ibid. *75* (Supplement): 949-960.

SMYTHE, N. (1970): On the existence of pursuit invitation signals in mammals. *Am. Nat. 104*: 491-494.

———————— (1977) : The function of mammalian alarm advertising social signals or pursuit invitation. ibid. *111*: 191-194.

SPILLETT, J. (1966) : A report on wildlife surveys in south and west India. *J. Bombay nat. Hist. Soc. 65*: 296-325.

———————— (1967) : A report on wildlife surveys in North India and Southern Nepal, The large mammals of the Keoladeo Ghana Sanctuary, Rajasthan. ibid. *63*: 602-607.

SUNQUIST, M. E. (1981) : The social organization of tigers (*Panthera tigris*) in Royal Chitawan National Park. *Smithsonian contrib. Zool. 336*: 1-98.

SWEENY, J., MARCHINTON, R. L. AND SWEENY, J. M. (1971) : Responses of radio-monitored white tailed deer chased by hunting dogs. *J. Wildl. mgmt. 35*: 704-716.

TRIVERS, R. L. (1971) : The evolution of reciprocal altruism. *Q. Rev. Biol. 46*: 35-57.

VAN LAWICK, H. (1971) : Wild dogs. *In* Innocent Killers, pp. 47-101. H. and J. Van Lawick Goodall, Collins, London.

WESLEY, D. G. (1977) : Census of wild animals in Bandipur Tiger Reserve. *My Forest. 13*: 15-19.

WRIGHT, B. (1960) : Predation on big game in Africa. *J. Wildl. mgmt. 24*: 1-15.

YAHNER, R. H. (1980) : Barking in a primitive ungulate, *Muntiacus reevesi*: function and adaptiveness. *Am. Nat. 116*: 157-177.